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Metabolism, Energetics, and Thermoregulation During Brooding of Snakes of the Genus *Python* (Reptilia, Boidae)

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(Plates I-II; Text-figures 1-24)

A study was made of various aspects of the metabolism and energetics of pythons in which particular attention was given to brooding females.

Gas exchange was measured at different temperatures with an open respirometric system equipped with an infrared carbon dioxide analyzer and a paramagnetic oxygen analyzer. Temperatures were measured with copper-constantan thermocouples connected to a potentiometric recorder. Gas exchange and temperature were measured and recorded continuously during periods of experimentation. Length-weight data of pythons were recorded in the New York Zoological Park and from information sent by other individuals and institutions. An energy budget was constructed from caloric determinations of ingested and egested material from several pythons.

Determinations of standard metabolism of pythons showed that their metabolic rates increase directly with temperature. At given temperatures metabolic rate per unit weight varies inversely with weight.

Heat production of *Python curtus, P. m. molurus, P. m. bivittatus,* and *P. reticulatus* at 26.0°C to 28.4°C is proportional to the two-thirds power of weight.

Heart beats of *Python molurus* increased from only 3/minute to 5/minute from 17°C to 26.5°C, but increased to 16/minute at 33°C. The pattern of increase paralleled that of oxygen consumption so that the oxygen pulse varied only slightly over the whole temperature range (range of O_2 pulse $= 2.19 \times 10^{-2} - 2.96 \times 10^{-2}$ ccO_2 beat^{-1} kg^{-1}).

Metabolic response to a 15°C temperature change was determined for *Python molurus* and *P. reticulatus.* Both species showed an initial metabolic rise with increased temperature from about 5 ccO_2 kg^{-1} hr^{-1} to 40 ccO_2 kg^{-1} hr^{-1} within 2 days but *P. molurus* dropped to 20 ccO_2 kg^{-1} hr^{-1} within 5 days, while *P. reticulatus* remained at the high level. When temperature was dropped to the low level, *P. molurus* showed a slight metabolic undershoot before returning to the original metabolic level. *Python reticulatus* did not show this undershoot.

A female Indian python *(Python m. bivittatus)* laid eggs in 1965 and 1966. During both brooding periods she produced sufficient additional heat by muscular contraction so that her body temperature was maintained above ambient. Temperature differentials of up to 5°C were recorded. The muscular contractions began when the ambient was below 33°C, and increased in frequency with decreasing temperature. Correlated with the decreasing temperature and increasing frequency of contractions was an increasing metabolic rate. At temperatures of about 25°C, the metabolic rate was about ten times the standard level. As the frequency of contractions increased, the python changed the

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shape of her coil around the eggs decreasing the surface area-to-volume ratio, thus aiding the maintenance of the temperature differential by decreasing the rate of heat loss.

A female *Python m. molurus* showed false brooding behavior over a period of several months and finally developed respiratory difficulty and was euthanized. Metabolic measurements made during parts of the false brooding corresponded with results from the above brooding python. Evidence from the true and false brooding points to a hormonal involvement in preparation for the brooding metabolic response to temperature.

Evidence is given for the occurrence of physiological thermoregulation during brooding in *Python curtus* and *Chondropython viridis* and its lack in *P. reticulatus* and *P. sebae*.

Energy budgets for three hatchling *Python curtus* over a two year period indicated that in normally growing animals about 10 percent of the food energy consumed was wasted as intestinal or renal waste; about 65 percent was used for maintenance and movement and about 25 percent went into growth.

Available data are presented to support the hypothesis that although *Python molurus* and *P. reticulatus* are sympatric over much of southeast Asia, the limiting factor for northern distribution is the ability of *P. molurus* to thermoregulate by physiological means during brooding and the lack of this ability in *P. reticulatus*.

INTRODUCTION

PHYSIOLOGICAL THERMOREGULATION during brooding in pythons has been suspected since 1832 when Lamarre-Picquot (1835) read a paper to the French Academy which stated that the Indian rock python *(Python molurus)* produces internal heat to aid egg incubation. A committee of the French Academy rejected Lamarre-Picquot's statements as being "hazardous and dangerous." Valenciennes (1841) and Lamarre-Picquot (1842) reported on new observations of the above phenomenon but Dumeril (1842) attributed the heat to decaying eggs. Additional reports of brooding in large pythons were made by Sclater (1862), Wray (1862), Forbes (1881), and Lederer (1944). Reports on brooding of smaller pythons have been made by Noble (1935) and Kratzer (1962). Krogh (1916) was prepared to make metabolic measurements of a brooding python in the Copenhagen Zoo but was denied permission by zoo officials. Benedict (1932) made temperature measurements of a brooding python over the period of one working day. More recent observations of heat production during brooding in pythons were made by Stemmler-Morath (1956).

In evaluating the above literature, the cases of brooding that also reported internal heat production have been found to be questionable on some grounds, e.g., inadequate temperature measuring devices, poorly-controlled experiments or insufficient data to justify the conclusions. Therefore, when Dowling made observations and temperature measurements with adequate temperature measuring devices under controlled conditions on two species of pythons *(Python molurus bivittatus and P. sebae)*, he was justified in claiming the existence of internal

heat production in *P. m. bivittatus* (Brattstrom, 1965; Dowling, 1960; Pope, 1965). These observations led us to the initiation of a more complete study of brooding and metabolism in pythons. This paper represents a part of the results of this study (Hutchison, Dowling, and Vinegar, 1966).
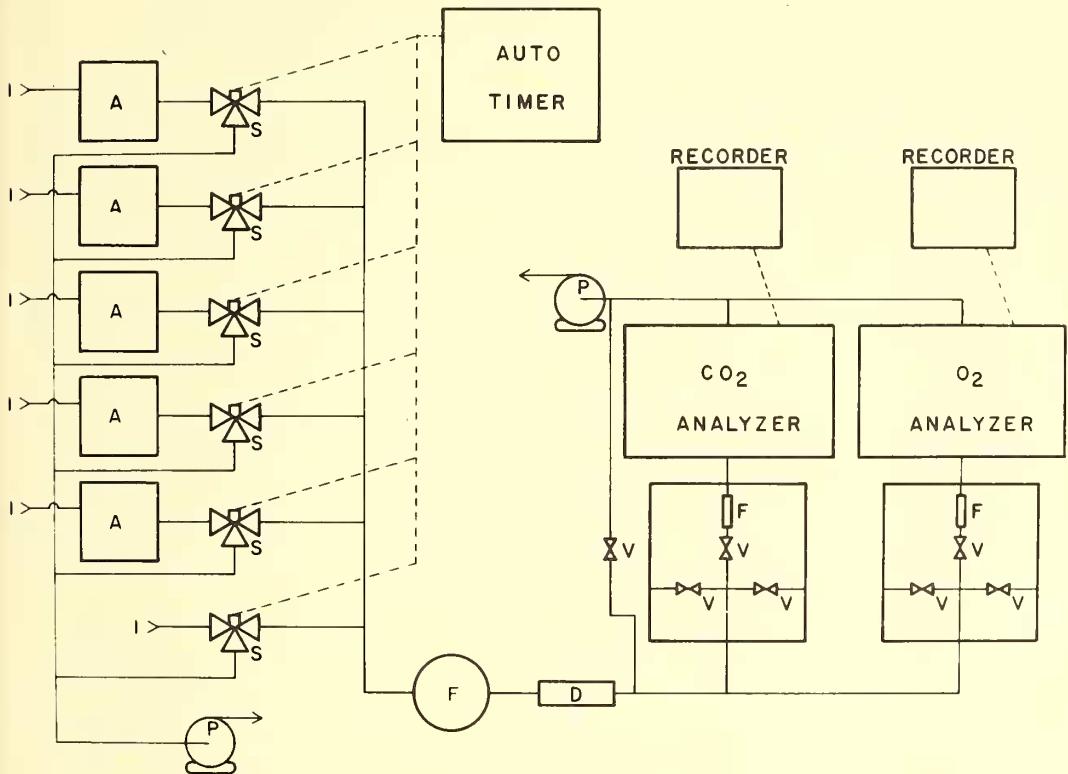
MATERIALS AND METHODS

Gas exchange was measured by an open system of respirometry. Animals were placed in individual plastic chambers through which room air was drawn. The air drawn from the chamber was analyzed for oxygen with a Beckman Model F3A3 analyzer and for carbon dioxide with a Beckman Model 15A infrared analyzer. Room air was analyzed periodically as a check against the chamber air. Flow rate was monitored with a wet-test flow meter. Air was drawn through the whole system with a pump. The outgoing chamber air passed through a three-way solenoid valve and then to a manifold before going through the analyzers. The solenoid valves were activated in sequence by an automatic sequencing timer; thus several chambers could be sampled automatically in sequence. A diagram of the system is shown in text-fig. 1.

Calculations of oxygen consumption were made using the formula derived by Depocas and Hart (1957) for open circuit systems where CO_2 and O_2 are monitored:

$$\dot{V}_{O_2} = (\dot{V}_I P_{I_{O_2}} - (\dot{V}_I + \dot{V}_{CO_2})\, P_{E_{O_2}})/P_B - P_{E_{O_2}}$$

where $\dot{V}_{O_2}$ is the oxygen consumption of the animal per hour, $\dot{V}_{CO_2}$ is the CO_2 production per hour, $\dot{V}_I$ is the volume of air flowing into the chamber per hour, $P_{I_{O_2}}$ is the partial pressure of oxygen in the air flowing into the chamber, $P_{E_{O_2}}$ is the partial pressure of oxygen in the air flowing out of the chamber, and P_B is the barometric pressure.

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TEXT-FIG. 1. Diagram of apparatus for measuring gas exchange. The symbols are as follows: A, animal chamber; D, drying tube; F, flow meter; P, air pump; S, three-way solenoid valve; V, flow control valve.

The room in which the experiments were performed was of double wall construction, with insulating material between the two walls. Temperature was controlled within $\pm 1°C$ with a system, composed of two air conditioners and a heater, which was thermostatically controlled and operated in opposition for fine control of temperature. The larger of the two air conditioners produced the initial drop in temperature for large temperature changes; the smaller unit then was adequate for maintaining the temperature.

Temperatures were recorded from copper-constantan thermocouples connected to a Leeds and Northrup Speedomax G 24-channel potentiometric recorder. Thus, 24 different temperatures could be monitored simultaneously with print-out for all channels appearing every 72 seconds.

Heart rates were recorded by taping small (50 mm²) pieces of fine mesh bronze screening with wires attached, on the venter anteriorly and posteriorly to the heart of the animal. Electrode jelly was used for making good electrical contact. Each of the two wires attached to the pieces of screening were connected to a miniature phone plug. The phone plug was then inserted into a jack at the end of a long, shielded cable which was attached to a Heathkit Impscope. Heart rates were determined by observing the beats on the Impscope and timing their frequency with a stop watch. Rates were not measured until at least one hour after the electrodes had been placed on the animal.

Information on weights and lengths of pythons were obtained from several sources. Animals at the New York Zoological Park (NYZP) were measured and weighed at varying intervals. Additional information was obtained by writing to other zoos and individuals who kept pythons. Weights also were taken of all pythons at the NYZP prior to all metabolic measurements.

Surface areas of pythons that died at NYZP were determined by carefully skinning the animal without pulling on the skin. The skin was placed on brown paper and traced. Areas of

small skins were determined with a K & E Compensating Polar Planimeter. Large skin areas were determined by weighing samples of the brown paper of known area and extrapolating the area of the skin from the total weight of the tracing. Measurements of the circumference of the animal were made at various points along its length before skinning to determine the degree of stretching; when the skin was placed on the tracing paper these measurements of circumference were maintained as closely as possible. Because the animal is truncated at both ends, it would be expected that the length of the skin would be greater than the actual length of the animal. However, since the length of the skin rarely exceeded the original length by more than a foot — even in the case of large animals — it is assumed that stretching was minimal.

Results and Discussion

Standard Metabolism of Pythons

Oxygen consumption of *Python curtus, P. molurus,* and *P. reticulatus* was measured at several ambient temperatures. Text-figs. 2 to 4

show the results of these measurements for animals of various weights. The data indicate increasing metabolic rate with increasing temperature and higher metabolic rates per unit weight for smaller animals.

Heat Production-Weight Correlation in Snakes

Galvão et al. (1965) dealt with heat production in relation to body weight and surface area in a number of tropical snakes. After converting oxygen consumption to heat production by using 4.8 calories as the equivalent of one ml of consumed oxygen, they plotted hourly heat production as a function of weight. Their experiments were performed at about 21.5°C but full acclimation information is not provided. Data for 16 boids of three species *(Boa constrictor amarali, Eunectes murinus,* and *E. notaeus)* gave the regression equation, calories/hour = 0.04 weight[1.09]. They compared these data with data from Benedict (1932) for 12 boids of four species *(Boa constrictor, Epicrates angulifer, Python molurus bivittatus,* and *P. recticulatus)* measured at 19.5°C to 23.3°C. These data
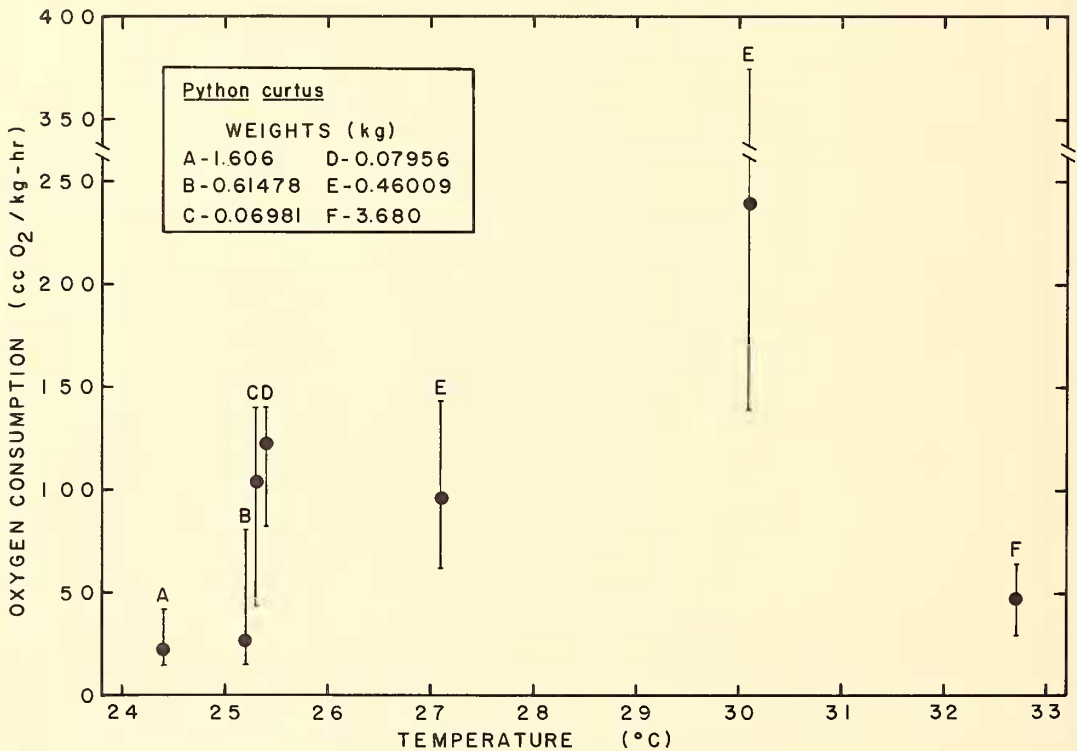
Text-fig. 2. Oxygen consumption of *Python curtus* at various ambient temperatures. Circles, means; vertical lines, ranges.

produced the equation, $C = 0.02W^{1.12}$. The two equations are not significantly different. The regression coefficient is not significantly different from 1.0, indicating that the metabolism is directly proportional to weight and not to the 0.67 power of the weight.

We did not have sufficient data for animals of different weights at 21°C for direct comparison with the above data. Therefore, a regression of metabolism on weight was calculated for data from ten boids of three species *(Python curtus, P. m. molurus, P. m. bivittatus,* and *P. reticulatus)* at 26.0°C to 28.4°C. These calculations resulted in the equation, $C = 1.975W^{0.664}$ where metabolism is, indeed, proportional to weight to the 0.67 power. For a comparison with Benedict's data, values for ten boids at 27.1°C to 29.1°C were taken from his work. These include eight of the animals and all four species used by Galvão et al. (1965) to calculate the regression at 19.5°C to 23.3°C The equation obtained was, $C = 0.395W^{0.852}$. The exponent is not significantly different from 0.664 figure obtained

in this study or from the values of 1.09 and 1.12 calculated by Galvão for his data at 21.5°C or for Benedict's data at 19.5°C to 23.3°C. All four regression equations discussed above and the individual values from this study are shown in text-fig. 5.

The relation between metabolism and weight depends on the temperature at which the metabolism is measured. It is also likely that a better comparison could be made, if the data were calculated for single species, rather than lumping together data from several species of two subfamilies (Pythoninae and Boinae).

Baldwin (1930) gave oxygen consumption data at 20°C for 13 specimens of *Pituophis sayi* weighing 272 grams to 835 grams. No data were given on the acclimation conditions. By converting the oxygen data to calories per hour and calculating a regression of heat production on weight, we obtained the equation, $C = 8.961W^{0.458}$. The data are highly variable, the 95 percent confidence limits on b being ± 0.797. A "t" test on b ($S_b = 0.362$) was not significant
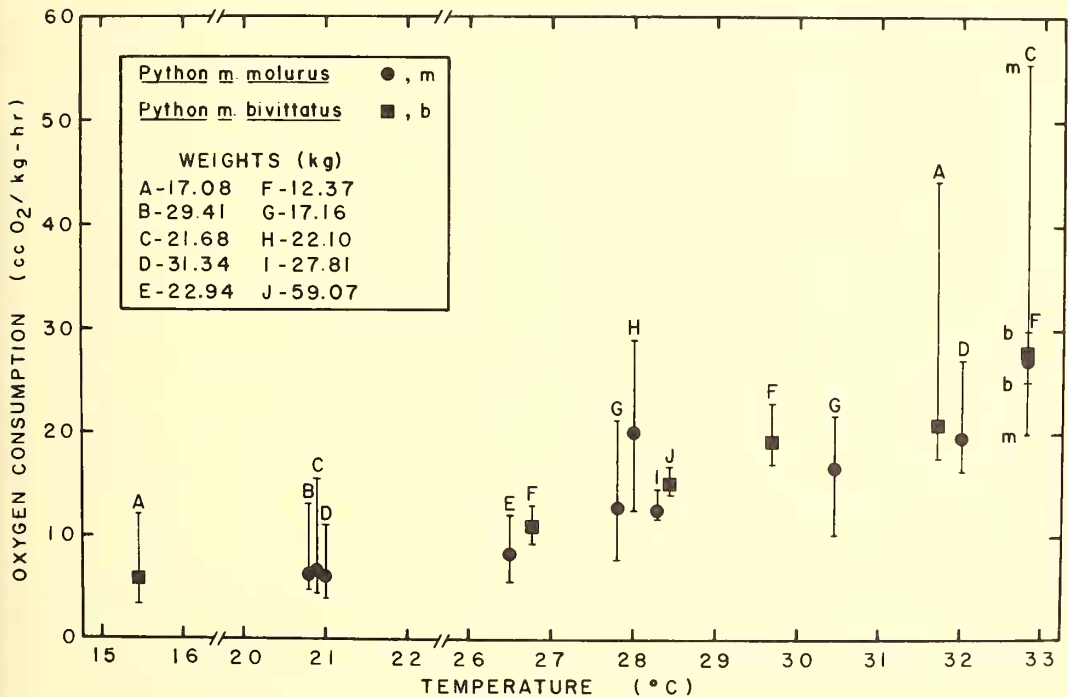
TEXT-FIG. 3. Oxygen consumption of *Python molurus* at various ambient temperatures. Circles, means; vertical lines, ranges.

(P < 0.20). Unfortunately, Baldwin provided no information that gives any clue to the source of the variability of the data.
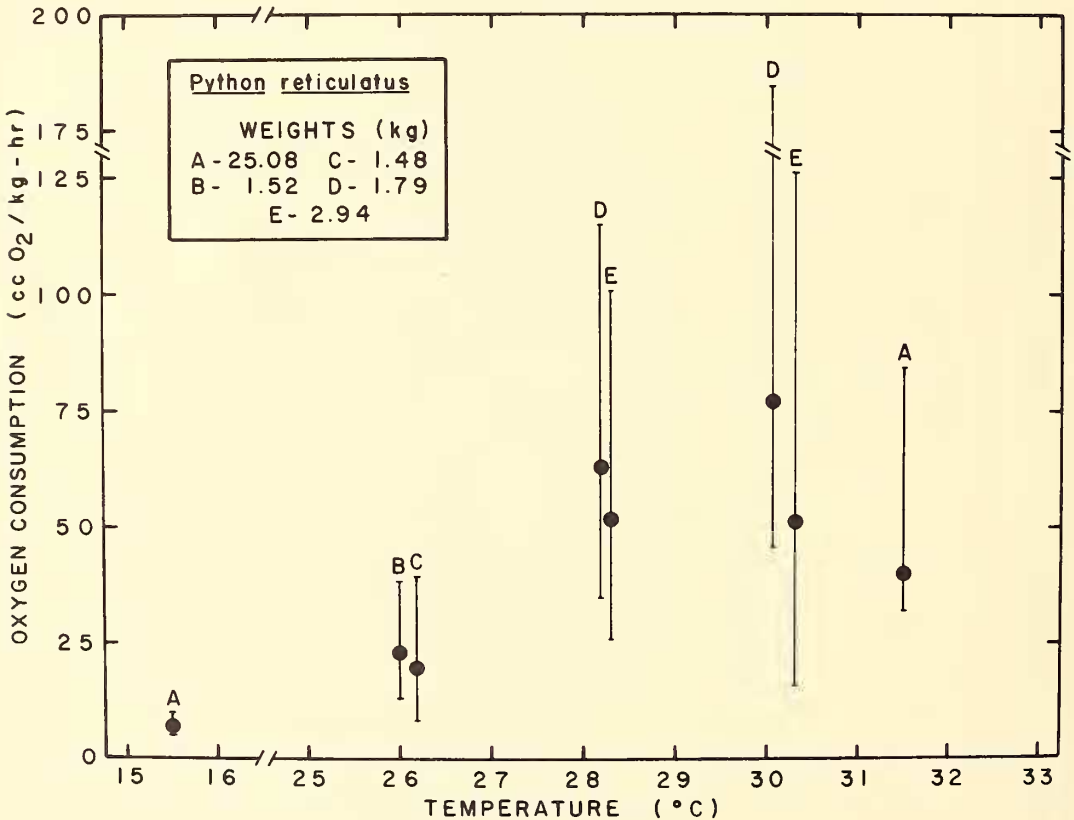
Heart Rates and Oxygen Pulse

Difficulty was encountered in obtaining heart rates from pythons. The time interval necessary for the animals to settle down after having the EKG leads placed on them also provided sufficient time for them to work the leads off. In spite of this problem heart rates were obtained for *Python molurus* acclimated to several temperatures. Rates varied from about three per minute at 17°C to about five per minute at 26.5°C. At 33°C the rate had increased to about 16 per minute (text-fig. 6). The response of heart rate to temperature apparently parallels the increase of oxygen uptake with temperature. Oxygen uptake increases from about 5 cc kg^{-1} hr^{-1} at 15.5°C to 12 cc kg^{-1} hr^{-1} at 27°C. The rate of increase then rises until the uptake is about 30 cc kg^{-1} hr^{-1} at 33°C (text-fig. 3). This correlation is shown more readily when the data are calculated as oxygen pulse (Table 1); with increasing temperature the heart rate increases proportionately with oxygen consumption and oxygen pulse remained fairly constant.

Jayasinghe and Fernando (1964) found a rate of 40 beats per minute for *Python molurus*. They failed to report either the acclimation or the measurement temperatures. The size of the animals was given as between 10 feet and 20 feet (three meters to six meters). Animals of these lengths could weigh between 10^4 grams and 10^5 grams. Therefore, without specific temperature and weight information, no direct comparison can be made with these data.

Heart rates of a 4313 gram, male boa constrictor, *Constrictor* [= *Boa*] *c. constrictor* were given by Clarke and Marx (1960). The snake was kept at 23°C to 27°C for some time before the measurements were made. Heart rates were taken over a four-hour period during which the temperature was dropped from 23°C to 18°C and the heart rate dropped from 15 beats to 12 beats per minute.

TEXT-FIG. 4. Oxygen consumption of *Python reticulatus* at various ambient temperatures. Circles, means: vertical lines, ranges.

TABLE 1.
HEART RATE AND OXYGEN PULSE DATA FOR *Python molurus.*

| Temp. (°C)	O₂ Cons. (cc kg⁻¹ hr⁻¹)	Heart Rate (beats/hour)	O₂ Pulse (ccO₂ beat⁻¹ kg⁻¹)	Snake Wt. (kg)
16.9	5.86	198	2.96×10^{-2}	17.08
20.8	6.40	240	2.67×10^{-2}	29.41
20.9	6.58	300	2.19×10^{-2}	21.68
26.5	8.37	300	2.79×10^{-2}	22.94
32.8	27.07	960	2.82×10^{-2}	21.68

Rebach (1969) measured heart rates of boa constrictors weighing from 0.393 kilograms to 8.51 kilograms at temperatures of 20.0°C and 32.2°C. Rates at 20.0°C were 6.4 (5.0-8.0) beats per minute and at 32.2°C were 23.9 (13.0-30.0) beats per minute. When the smaller size of these snakes is considered, the measured heart rates are in good agreement with those of the pythons measured in the present study.

Mullen (1967) measured heart rates of several temperate zone lizards and snakes, all of which are of small size compared to pythons. Mean heart rates for the snakes varied from about 43 beats per minute at 22°C to about 95 beats per minute at 30°C. These rates are considerably higher than the rates found for the Indian python but the greater mass of the python probably accounts for its lower heart rates. Bartholomew and Tucker (1964) demonstrated an inverse correlation between heart rate and weight in varanid lizards; this correlation also occurs in other animals.
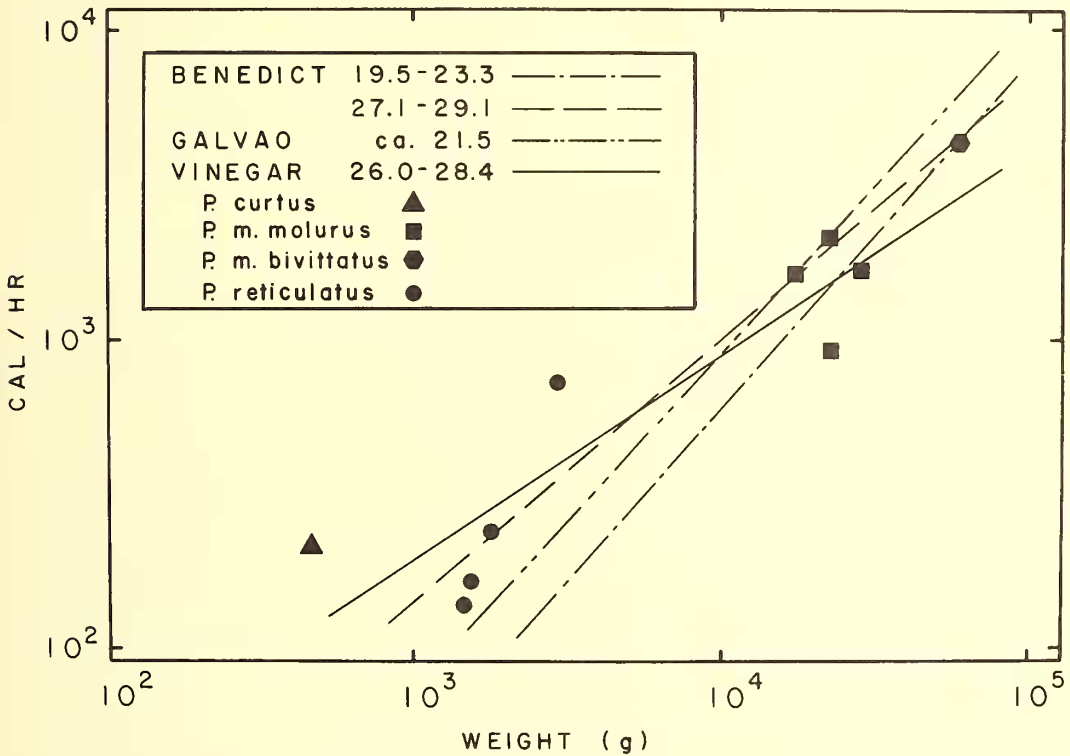
TEXT-FIG. 5. Correlation of heat production with weight of boids based on the data of several investigators. Regression equations obtained by the method of least squares are as follows: Benedict (19.5-23.3), C = 0.02W^1.12; Benedict (27.1-29.1), C = 0.395W^0.852; Galvao (21.5), C = 0.04W^1.09; Vinegar (26.0-28.4), C = 1.975W^0.664. Individual points are plotted for data from this study only.
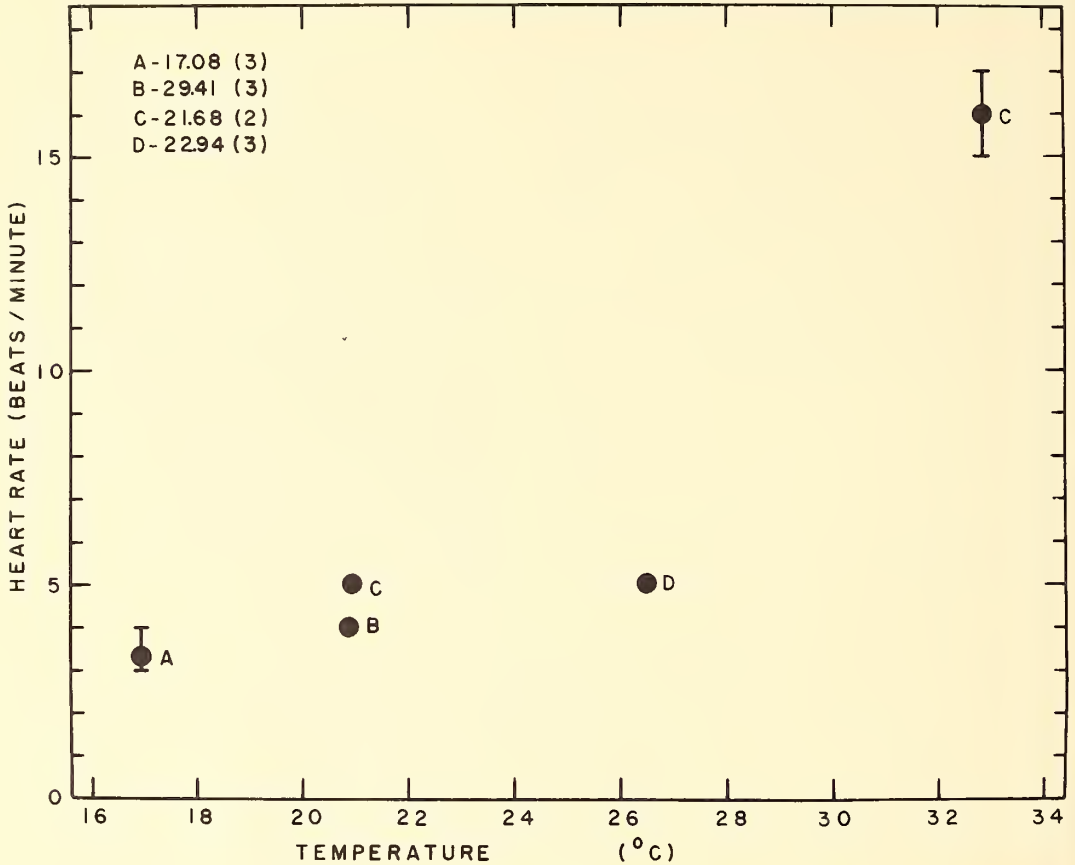
TEXT-FIG. 6. Heart rates of *Python molurus* at several ambient temperatures. Weights and sample size for each point are shown in the upper left of the figure. Circles, means; vertical lines, ranges.

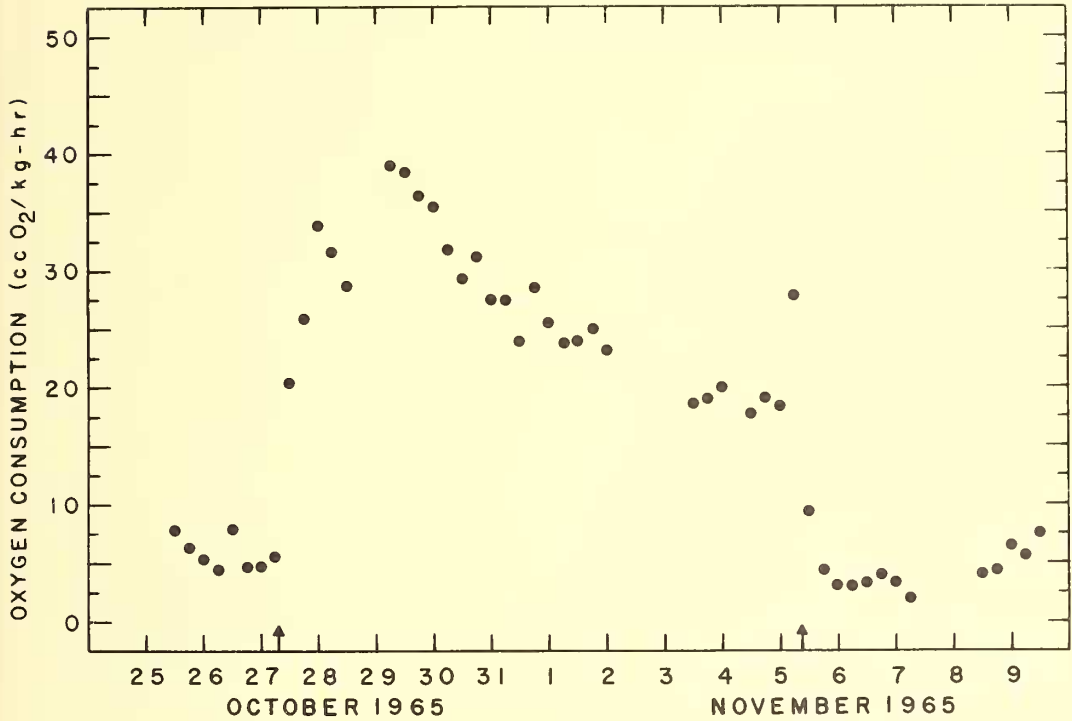Metabolic Responses to Temperature Change

Specimens of *Python molurus bivittatus* (NYZP No. 630514) and *P. reticulatus* (NYZP No. 640670), 17.08 kilograms and 25.08 kilograms, respectively, were subjected to rapid changes in temperature of about 15°C. The animals were initially acclimated to the lower temperature for a two-week period. Temperature was then increased, kept at the high setting for nine days and finally returned to the low setting. Gas exchange was measured over the whole period (text-figs. 7 and 8). The metabolic response to temperature rise was slightly different in each of the animals. *Python molurus* showed an initial increase from about 5 cc kg^{-1} hr^{-1} to 40 cc kg^{-1} hr^{-1} within two days and then a gradual drop to 20 cc kg^{-1} hr^{-1} within five days. *Python reticulatus* showed the same initial increase but remained at a level of about 35-40 cc kg^{-1} hr^{-1} for the nine day period. Decreased temperature seemed to produce a slight metabolic undershoot in *P. molurus,* while *P. reticulatus* returned immediately to its initial level.

Further measurements are necessary before any conclusions can be reached regarding the consistency of these responses.

Brooding Metabolism of *Python molurus bivittatus*

An Indian python *(Python molurus bivittatus,* NYZP No. 630514), 14.25 kilograms in weight and 2.7 meters in length, laid 23 infertile eggs on or about February 15, 1965. The animal was found coiled around the eggs on February 18 and was transferred, without disturbing her or the eggs, to a respiration chamber in a temperature controlled ($\pm$ 1°C) room. Measurements of gas exchange, temperatures, and contraction rates were made for the 30-day period that the python remained on the eggs. Additional gas exchange measurements were taken 40 days after the end of the brooding period to obtain non-brooding values. Oxygen consumption calculations were based on the weight of the snake at 14.25 kilograms during brooding and at 12.37 kilograms during non-brooding.

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TEXT-FIG. 7. Metabolic response to temperature change in a 17.08 kilogram *Python molurus bivittatus.* Temperature changed from 15.4° to 31.7°C on October 27 and back to 15.4°C on November 5 (arrows).

Oxygen consumption during non-brooding was typical of an ectothermic animal, decreasing with decreasing temperature (text-fig. 9, lower curve); but oxygen consumption during brooding was similar to that of endothermic animals (text-fig. 9, upper curve). At about 33°C, the metabolic rate of the python is approximately the same during brooding and non-brooding. However, the oxygen consumption of the brooding animal increased when the temperature was decreased from 33°C to 25.5°C. Thus, 33°C appears to be analogous to the "lower critical temperature" of birds and mammals. The analogy is enhanced further by the onset of muscular contractions which accompany the increased metabolism at temperatures below 33°C. The frequency of contractions increases with decreasing temperature and increasing metabolism (text-fig. 10). A similar correlation exists between the temperature differential between animal and air and the contraction rate (text-fig. 11). A maximum temperature differential of 4.7°C was maintained at an ambient temperature of 24.8°C (text-fig. 12). A full account of the data for this brooding was given by Hutchison, Dowling, and Vinegar (1966).

On February 15, 1966, a specimen of *Python molurus bivittatus* (NYZP No. 630514) was found coiled in a corner of an exhibit cage. One egg, which was opened and found to be infertile was noted beside her. No other eggs were laid at the time. The animal was taken to the laboratory and placed in a respiration chamber. She weighed 17.25 kilograms (including the ejected egg). Twenty-one additional eggs were laid during the night of February 16-17, 1966. Respiration, temperature, and contraction rate data were collected as during the brooding period of the previous year. Several eggs were removed during the course of brooding as they started to turn yellow. On March 28, 1966, the remaining eggs, which were all infertile, were removed from the female as all signs of regular contractions had stopped. Irregular contractions were noted until April 8, 1966.
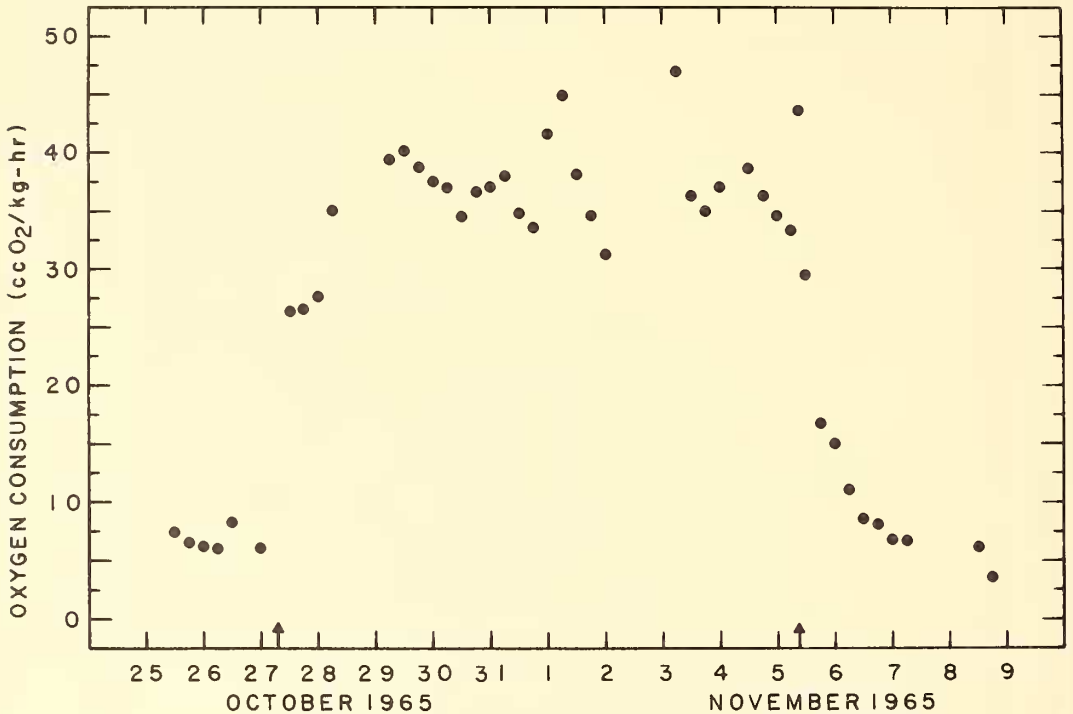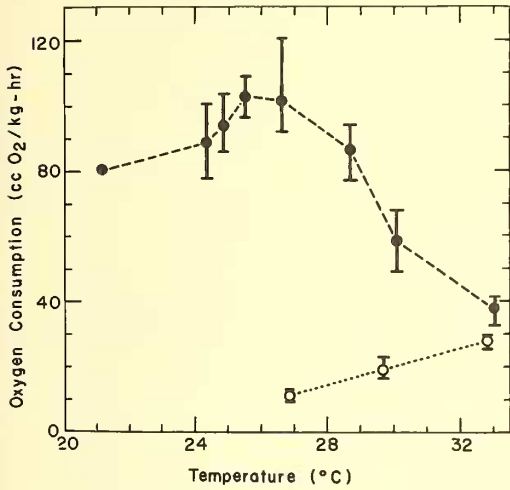
TEXT-FIG. 8. Metabolic response to temperature change in a 25.08 kilogram *Python reticulatus*. Temperature changed from 15.5° to 31.5°C on October 27 and back to 15.5°C on November 5 (arrows).

Although tidal volume could not be determined quantitatively, qualitative observations were made. The number of inspirations per minute increased with increasing contraction rate. Contraction and breathing rates were: 2, 2; 9, 4; 33, 6; 37, 6. The normal inspiration rate in a large python is about two per minute. Although the frequency of inspirations did not increase greatly with increasing contractions, the tidal volume did increase. The breaths of six per minute were quite noticeably deeper than those at two to four per minute. Measurements were also made of the height and basal width of the snake's coil at different contraction rates. Calculations of volume and area were made assuming the coil to be a solid cone. A brooding *P. m. bivittatus* is pictured in Plate I. Table 2 shows the calculated data; the surface area calculated includes that part in contact with the substrate. Surface area to volume ratios decreased with increasing contraction rates. The metabolic data were similar to those obtained in the previous year. Text-fig. 13 shows the oxygen consumption-contraction rate data for the two years. Data for contraction rates at various temperature differentials are plotted in text-fig. 14, and body temperature-ambient temperature data are shown in text-fig. 15. During most of the 1966 brooding, a 17.1 kilogram specimen of *P. m. molurus* (NYZP No. 640578), was kept in a second respiration chamber. Its metabolic responses to temperature were also determined. Data for the two animals are shown for an 11-day period at various temperatures in text-fig. 16.

False Brooding Behavior in a Female
Python molurus molurus

On May 31, 1966, a specimen of *Python molurus molurus* (NYZP No. 640578) was seen contracting at an uneven rate in a manner similar to a brooding python. Since contractions of this type had been seen previous to the last two egg layings of *P. m. bivittatus* (NYZP No. 630514), it was assumed that No. 640578 would probably lay eggs within the following few days. The ambient temperature of the cage and surroundings of the python was about 27°C. It was transferred to the laboratory (at 31°C) and placed in one of the metabolism chambers so that she

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TEXT-FIG. 9. Oxygen consumption of a *Python molurus bivittatus* at different ambient temperatures. Upper curve: animal during brooding. Lower curve: same animal during non-brooding. Circles, means; vertical lines, range. (from Hutchison, V. H., H. G. Dowling and A. Vinegar, 1966).
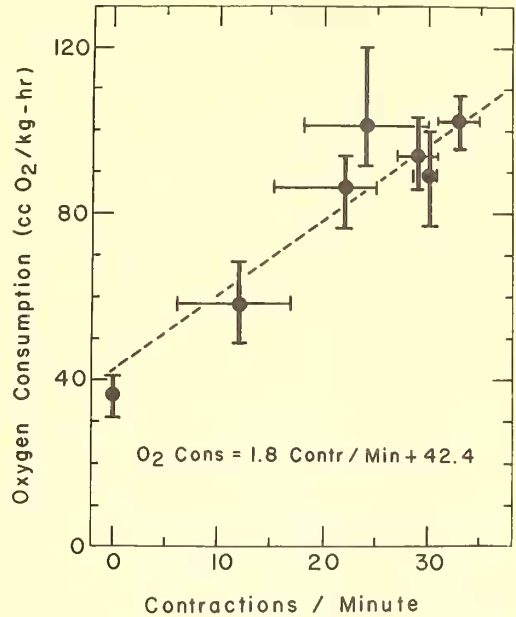
TEXT-FIG. 10. Correlation of rate of body contractions with oxygen consumption in a brooding *Python molurus bivittatus.* Dashed line and regression equation calculated by method of least squares. Circles, means; vertical lines, range of oxygen consumption; horizontal lines, range of contraction rate (from Hutchison, V. H., H. G. Dowling and A. Vinegar, 1966).
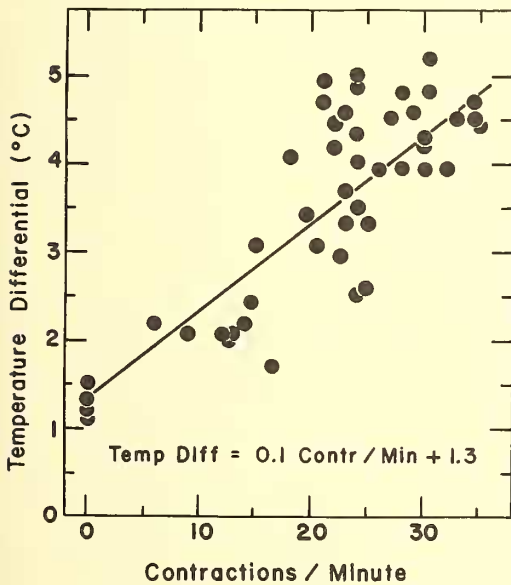
TEXT-FIG. 11. Correlation of contraction rate with temperature differential in a brooding *Python molurus bivittatus.* Line and regression equation calculated by method of least squares. Circles represent individual measurements (from Hutchison, V. H., H. G. Dowling and A. Vinegar, 1966).
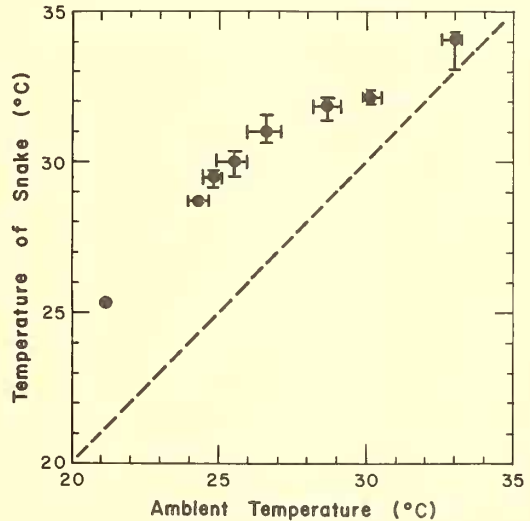
TEXT-FIG. 12. Correlation of body temperature of a brooding *Python molurus bivittatus* with ambient temperature. Dashed line indicates equal ambient and animal temperatures. Circles, means; vertical lines, range of animal temperature; horizontal lines, range of ambient temperature (from Hutchison, V. H., H. G. Dowling and A. Vinegar, 1966).

TABLE 2.
COIL SIZE DATA FOR A BROODING INDIAN PYTHON.

| T_B-T_A (°C)	Contraction Rate Per Minute	Coil Ht. (cm)	Coil Width (cm)	Coil Vol. (cm³)	Coil Area (cm²)	Area/Vol.
1.6	2-3	11	50	7198.13	4106.34	0.57
3.4	30	16	48	9649.15	3982.02	0.41
4.8	42-45	20	46	11077.26	3862.33	0.35

could lay her eggs there. Gas exchange measurements were made from June 13 to June 16 and July 2 to July 12, 1966. Ambient temperature was changed several times during these periods. No eggs were laid and the animal was removed from the laboratory on July 12, when muscular contractions were no longer observed. Occasional irregular contractions were noted until September 2. Offerings of food were consistently ignored. On October 6 the python was force fed one rat. A mucous discharge was seen coming from the mouth on October 25. The animal seemed to be having trouble breathing and was euthanized with nembutal on November 1. Autopsy confirmed that the animal was a female.

The contractions of the animal were more regular and the response to temperature change more pronounced from June 13 to June 16 than from July 2 to July 12 (text-fig. 17). A decrease in ambient temperature from 31°C to 26°C on June 14 resulted in an immediate increase in

metabolic rate. On July 5, a similar decrease from 32° to 25.5°C resulted in an initial decrease and then in an increase in metabolism, although not to the level reached on the earlier date. By this time the metabolic response to temperature change was slight. These observations and the irregular contractions seen in *P. m. bivittatus* (No. 630514) prior to egg laying suggest that physiological thermoregulation in pythons is under hormonal control. The irregular contractions in No. 630514 up to one week prior to egg laying suggest an increase of certain hormone levels to that required for thermoregulation. The sluggish response to temperature change in No. 640578 probably reflects a change in hormone level towards the normal non-brooding condition. This, however, does not explain the brooding behavior and thermoregulation in an animal that has not laid eggs. A possible explanation might be a malignancy affecting the brain area controlling the whole brooding response or the gland responsible for secreting a hormone involved in brooding. Since the normal brooding period is from one-and-a-half to two-months long, and since this animal continued to show irregular brooding behavior for over three months, further support is given to the malignancy hypothesis.

Brooding in Various Python Species
Python curtus

Noble (1935) described the laying of 16 infertile eggs and the brooding of a blood python, *Python curtus*. Temperatures reported were taken with a gas-filled mercury thermometer. All of the body temperatures reported were intermediate between the temperatures of the substrate and the air, and indicated that the snake had not developed an elevated body temperature. However, the substrate temperatures reported were 31.5°C, 31.8°C, and 32.2°C. These temperatures are in the vicinity of the lower critical temperature (33°C) found in the present study for *P. molurus*, therefore the "thermostat" of Noble's python may not have been "calling for heat." No conclusions regarding the ability or inability of *P. curtus* to thermoregulate can be drawn from Noble's observations.
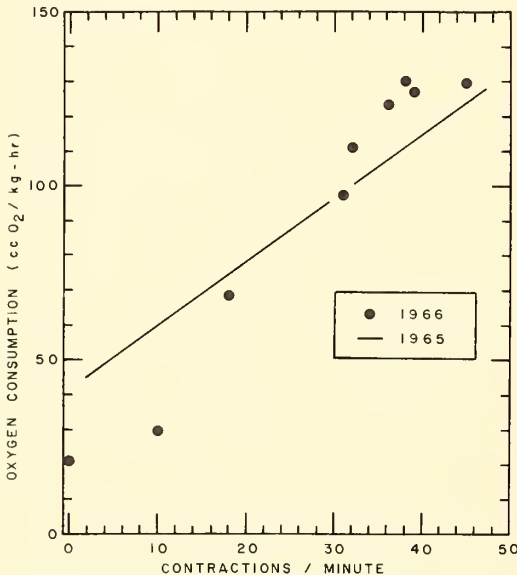
TEXT-FIG. 13. Correlation of rate of body contractions with oxygen consumption in a brooding *Python molurus bivittatus*. Regression line represents data from 1965 shown in Fig. 10. Circles represent data from the same individual for 1966.
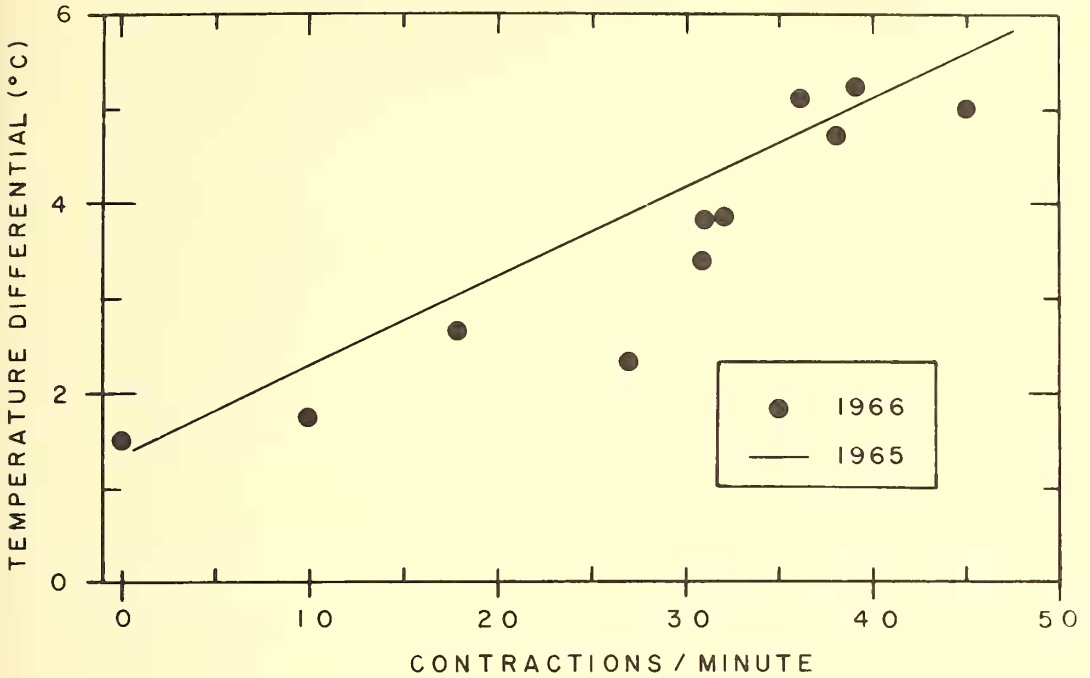
TEXT-FIG. 14. Correlation of contraction rate with temperature differential in a brooding *Python molurus bivittatus*. Regression line represents data from 1965 shown in Fig. 11. Circles represent data from the same individual for 1966.
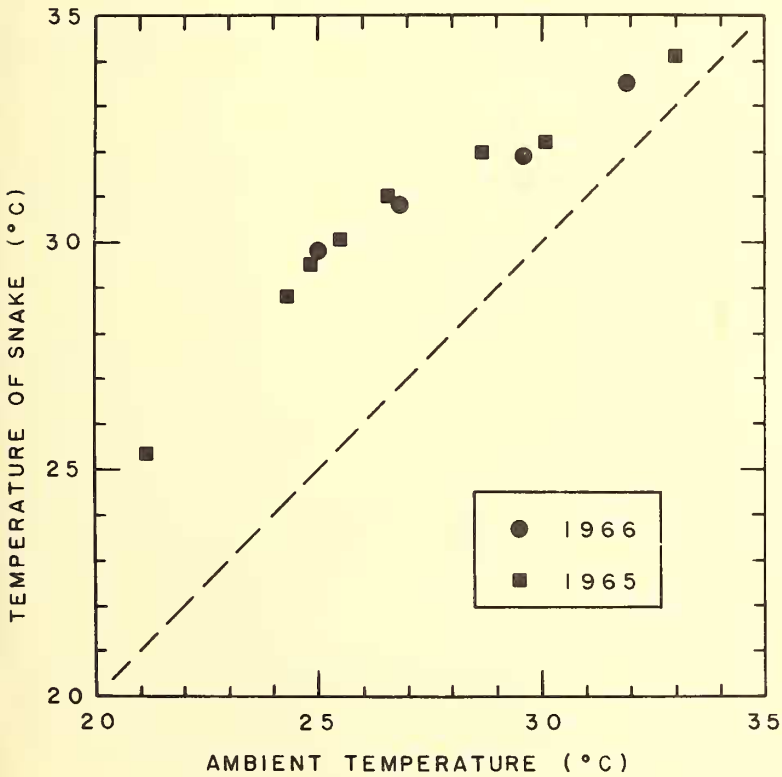
TEXT-FIG. 15. Correlation of body temperature of a brooding *Python molurus bivittatus* with ambient temperature. Dashed line indicates equal ambient and animal temperatures. Squares, data from 1965; circles, data from 1966.
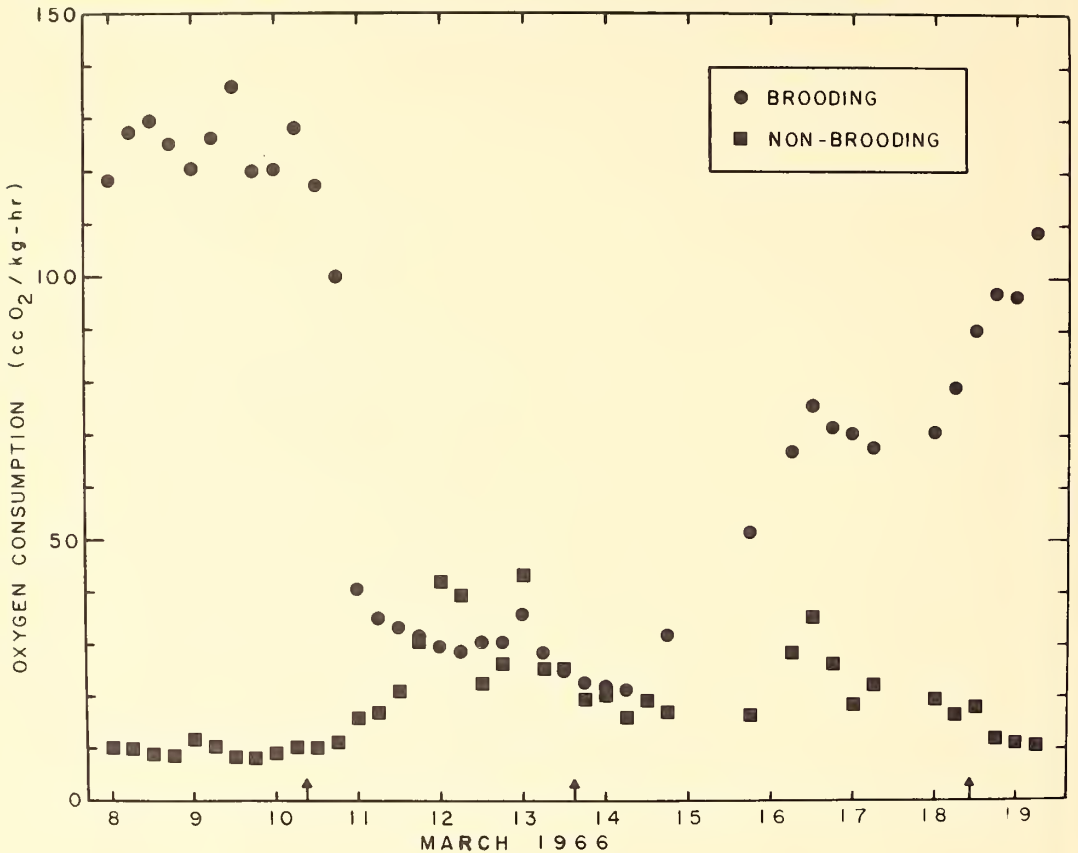
TEXT-FIG. 16. Oxygen consumption of brooding and non-brooding *Python molurus* under identical ambient temperatures. Temperature changed from 24° to 31.5° on 10 March, to 30° on 13 March and to 23.5°C on 18 March (arrows).

Additional definite information regarding the ability of *P. curtus* to thermoregulate physiologically while brooding its eggs was obtained during the present studies. A female blood python laid fertile eggs on May 29, 1965, while none of the project personnel was available. The animal was removed from her eggs at that time and would not return to them on May 31 when she was placed back with them. Nevertheless, on June 1 when she was placed in a room at about 27°C, she contracted her musculature at a rapid but irregular pace of about 27 contractions per minute. Irregular sporadic contractions had been noticed six weeks prior to egg laying. No further data were obtained from the python because normal brooding information could no longer be obtained. However, this evidence suggests a second species of python that has some ability to respond physiologically to decreases in ambient temperature while brooding eggs.

Chondropython viridis

Evidence exists for a third species having the ability to control its temperature while brooding.

Kratzer (1962) reported on mating and brooding of *Chondropython viridis*. After egg laying the female python showed muscular twitching at intervals of two to three seconds. The temperature of the substrate was reported at 28°C and that of the air, 26°C to 30°C. However, these temperatures were obtained a month or more before the eggs were laid. If the temperatures were about the same after laying, the observed contractions would be expected in an animal capable of such a response to temperature decrease.

Python reticulatus

Little information exists regarding brooding in *Python reticulatus*. Wall (1926) described various aspects of the biology of the reticulated python. In his section on brooding he stated that "Experiments prove that the dam's body temperature is not raised during this period." However, he did not state whose experiments these were or under what conditions they were performed. Lederer (1944) made some observations on a brooding animal of this species and
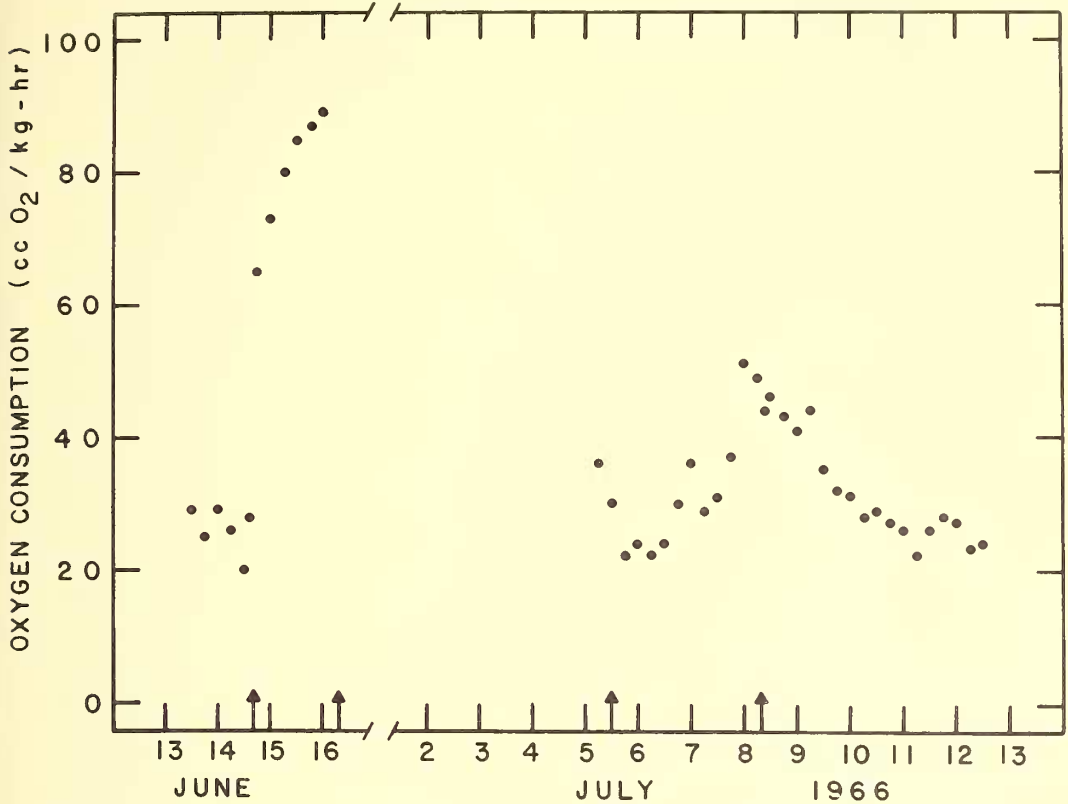
TEXT-FIG. 17. Oxygen consumption of a *Python molurus* showing false brooding behavior. Temperature changed from 30.5° to 26° on 14 June, to 33° on 16 June, to 25° on 5 July and to 30°C on 8 July (arrows).

found that the snake's temperature was close to that of the substrate which was several degrees higher than the air temperature. Unfortunately, the lowest substrate temperature reported was 32.2°C, which is the approximate critical minimum temperature for the Indian python. The animal, therefore, probably was not observed under conditions that would have elicited the thermoregulatory response.

Some information that may be more useful in determining whether *P. reticulatus* is capable of maintaining its temperature above that of the environment by physiological means was provided by a visitor from Malaya to the New York Zoological Park. The information was given to Assistant Animal Manager Peter Brazaitis by the visitor, K. J. Sims. Sims had a 20-foot python that laid 67 eggs in an outdoor enclosure. Since Sims worked up to 14 hours a day, many of his observations. were made in the evening when the temperature was already cooler. During all of his observations he never saw the animal undergo muscular contractions. These observations suggest that the reticulated python lacks any physiological thermoregulatory ability.

On January 29, 1968, a *P. reticulatus*, weighing 73.19 kilograms, laid 51 eggs at the New York Zoological Park. The animal died two days later so that little information was obtained. However, at no time did anyone see any signs of muscular contractions.

No other reports were found of *P. reticulatus* brooding in zoological gardens or in nature that would clarify the brooding situation in this species. The information that is available indicates that this species does not have the same thermoregulatory ability that has been demonstrated in *P. molurus*.

Python sebae

Brooding in *Python sebae* was reported by Sclater (1862). He made simultaneous temperature measurements of a 14-foot male and a 22-foot brooding female python. The eggs were laid on January 13 and were removed from the female on April 4. She had left the eggs only a few times during the whole brooding period. Temperatures between the coils of the male and female on each of four different days were:

74.8°F, 81.6°F; 74.0°F, 83.2°F; 76.0°F, 96.0°F; 77.6°F and 86.0°F (23.8°C, 27.6°C; 23.4°C, 28.5°C; 24.5°C, 35.6°C; 25.4°C, and 30.0°C). Air temperatures during each of the previous measurements were: 58.6°F, 65.4°F, 60.0°F, and 66.0°F (14.8°C, 18.6°C, 15.6°C, and 18.9°C). No conclusions regarding the physiological thermoregulatory ability of *P. sebae* can be reached on the basis of these date. Although the temperatures of the male and female pythons were both above the air temperature, no mention of the floor temperature was made except that the cage was heated by hot water pipes. It seems likely that the animals were warmed by conductive heat from the water pipes (probably during the night when the snakes are more active). The female would have retained heat better than the male because her larger size and coil around the eggs presented less surface area per unit mass for heat loss to the environment.

Fitzsimons (1930), in referring to brooding of pythons, stated: "At this period her blood rises to a temperature of 90° Fahrenheit, which is apparently, Nature's rule for the hatching of infant pythons." The source of this information was not stated. It is apparently a generalization that Fitzsimons made as a result of reading some of the early accounts of python brooding temperatures, since he referred to these accounts without giving the specific sources.

Benedict (1932) gave an account of respiration rates and temperatures of a brooding 4.6 meter specimen of *P. sebae* at the National Zoological Park in Washington, D.C. The measurements were made on one day only. Average respiration rates during the course of the day ranged from 2.0 to 3.1 breaths per minute. Three sets of measurements were made during the day. Temperatures of the gravel around the python ranged from 29.92°C to 32.82°C; of the air 10 centimeters to 15 centimeters above the floor, 29.20°C to 32.04°C; of the air 30 centimeters above the floor, 29.30°C to 32.02°C; of the air 60 centimeters above the floor, 29.14°C to 31.44°C; under the python, 32.07°C to 34.62°C: between folds of python, 33.33°C to 35.18°C. During the three sets of measurements Benedict recorded temperature differences between snake and environment of up to 3°C or 4°C. However, some information given by Benedict casts doubt on the validity of his conclusions. The incubating python was located near a glass window that was a few centimeters from the air in the corridor outside the cage. The air outside the cage was reported as 20.4°C.

In 1960, Dowling (1960 and unpublished data) observed two brooding female pythons. One was a 53.07-kilogram (including eggs)

specimen of *Python molurus* (NYZP No. 540616) and the other a 20.86 kilogram (including eggs) specimen of *P. sebae*. The former laid 53 eggs on April 6 and the latter laid 45 eggs on April 11. Temperatures of the animals, substrate, and air were taken at various times during the brooding period. Hourly readings for both animals were made from 0745 on April 29 until 0745 on April 30. The temperatures recorded for the animals and the adjacent substrate are shown in text-fig. 18. Text-fig. 18A shows that the body temperature of the *P. sebae* followed that of the substrate when the substrate temperature was lowered. Text-fig. 18B shows that the body temperature of *P. molurus* while brooding is relatively independent of the substrate temperature. Dowling noted that the Indian python contracted its musculature at a rate that was inversely proportional to temperature. No muscular contractions were seen in the African python. Text-fig. 19 shows the relationship between contraction rate and temperature differential (animal temperature minus substrate temperature). These data are presented for the above Indian python and for another individual (NYZP No. 510720) weighing 43.41 kilograms, including eggs laid on April 5, 1961. The African python was seen to leave its eggs during brooding and to go into the heated pool in the cage and later return to the eggs. It seems probable that the African rock python also lacks the thermoregulatory ability exhibited by the Indian python.

Morelia spilotes variegata

Cogger and Holmes (1960) produced good evidence to show that the carpet python *(Morelia spilotes)* regulates its temperature behaviorally. The animal basks in the sun and then forms a tight coil while resting. Heat was retained even through the night. However, if the following day was cloudy, the animal eventually came into equilibrium with the surrounding air. The data would have been more convincing if substrate temperatures had been given. The warmest temperature recorded for the snake on a sunny day was about 90°F (32.2°C), which is the lower critical temperature demonstrated for brooding Indian pythons. Cogger and Holmes suggested that *Morelia* may regulate its temperature similarly while brooding its eggs.

Egg Brooding in Various Reptiles

Reptile eggs get various degrees of care by the parent after being laid. Many eggs are merely laid in a hole in the ground or under the bark of a fallen log and left to the elements. Some animals lay their eggs in places that do not fluctuate much in temperature or humidity. One such
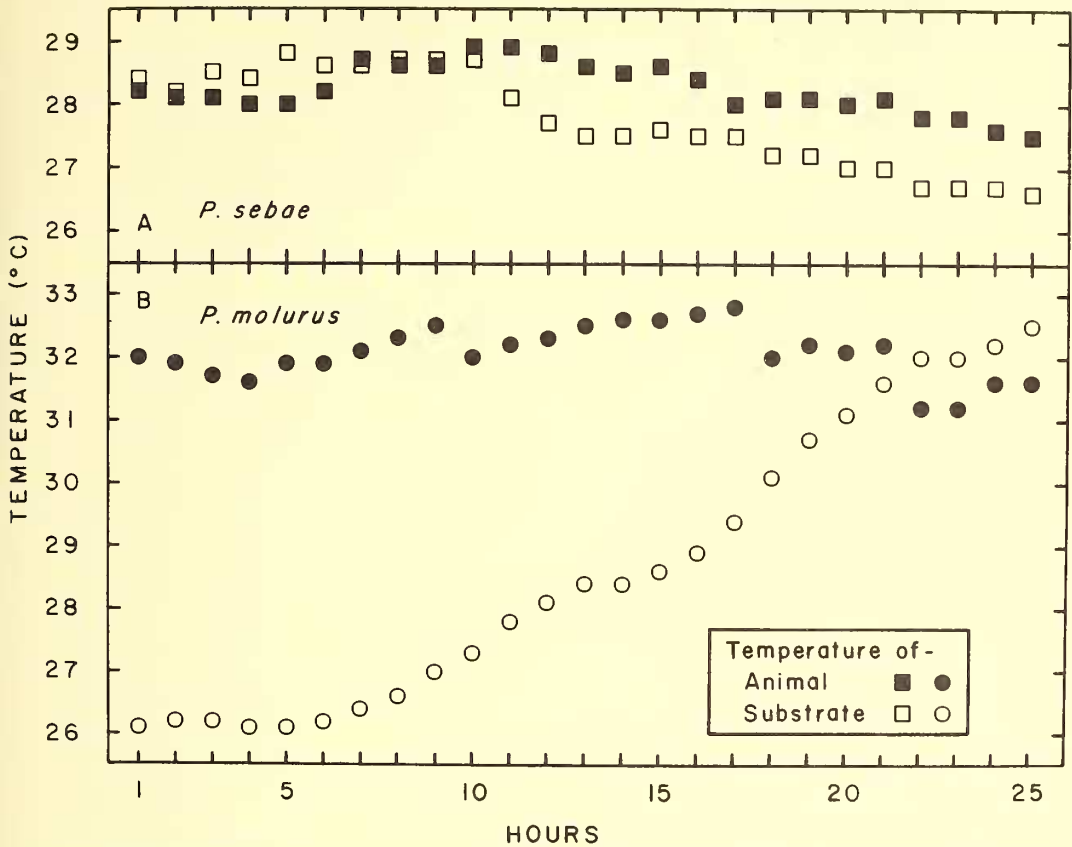
TEXT-FIG. 18. Body and substrate temperatures over a one day period for two brooding pythons *(Python molurus* and *P. sebae)*. Key to symbols in lower right of figure.

place is in termite nests. An account of temperature regulation in termite nests was given by Luscher (1961). The South American teid, *Tupinambis nigropunctatus,* lays its eggs in termite nests (Hagmann, 1906). *Gehyra pilbara,* an Australian gecko, not only lays its eggs in mounds of the termite, *Eutermes triodiae,* but also lives in the mounds, thus escaping the rigors of the surrounding desert (Mitchell, 1965). A small python, *Liasis childreni perthensis,* which reaches an adult length of 30 centimeters, is found also in the nest with *Gehyra.* Although Mitchell did mention that *Gehyra* is a food item of the python, no information was given as to whether *Liasis* also lays its eggs in the termite mound. Noble and Mason (1933) summarized the literature up to that time on various snakes and lizards that actually stay with or brood their eggs. While some of the animals may sun themselves between periods of brooding, their size makes it unlikely that they contribute any appreciable heat for the development of their eggs. Most cases presented seem to be examples of egg protection rather than egg incubation. Noble and Mason (1933) provided some of their own

data on brooding in *Eumeces fasciatus, E. laticeps,* and *Ophisaurus ventralis.* Body temperatures of *Eumeces* were reported to be 1.6°C to 3.2°C higher than that of the eggs. However, mention was made also of how quickly the body temperatures could change. This, along with the infrequency of temperature readings, casts doubt on any degree of thermoregulation existing for *Eumeces.* The authors concluded from similar infrequent data recordings that *Ophisaurus* probably does not have any thermoregulatory ability. A more detailed account of brooding in *Ophisaurus* was given by Vinegar (1968).

A detailed account of the manner in which the Nile monitor, *Varanus niloticus,* makes use of the nests of the termite, *Nasutitermes trinerviformis,* for incubation of its eggs in Natal, was given by Cowles (1930). Kopstein (1938) summarized several papers concerning the snake *Boiga drapiezii* and its laying of eggs in the nest of the termite, *Lacessititermes batavus.*

Energetics of *Python curtus*

No previous attempt has been made to consider a complete energy budget for a snake. With
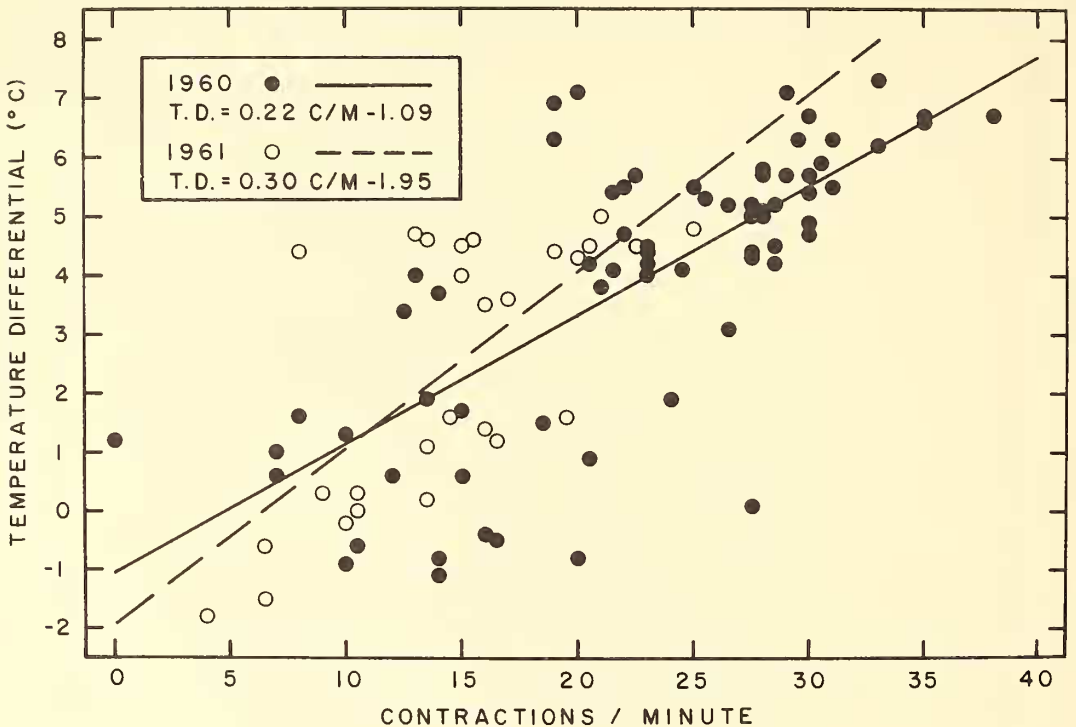
Text-fig. 19. Correlation of body contractions with temperature differential (body temperature − substrate temperature) for two different *Python molurus bivittatus*. Lines and regression equations calculated by method of least squares. Key to symbols in upper left of figure.

hope of accomplishing this, in August 1965 three hatchlings of *Python curtus* were placed in individual cages in a temperature-controlled room (27°C). The animals were kept at this temperature except for periods of several weeks when they were acclimated to different temperatures for measurement of gas exchange. A water bowl was kept in each cage. Food consisted of albino mice except for one snake which was fed rats after 14 months. The food was weighed before being fed to the snakes. After each defecation the pythons were weighed. Lengths were not taken because of the difficulty in getting the animals stretched out. The severe struggling of the animals would have injured them and probably made them stop feeding. The defecations and renal waste were frozen and later oven-dried, weighed, and the caloric content determined. Caloric content was also determined for mice and for a python (a young individual of *P. sebae*). The caloric value obtained from this animal was used to calculate the energy budget of *Python curtus,* but is a tentative value, to be replaced as soon as caloric determinations of a series of *P. curtus* can be made.

Caloric values were determined with a Parr Adiabatic Oxygen Bomb Calorimeter. Six determinations were made on each sample with the mean value being used as the caloric value of the sample.

Text-fig. 20 shows the growth of the three *P. curtus* over a period of two years (August 1965 to July 1967). A marked difference in growth rate is evident. Photographs taken on February 14, 1967, emphasize this difference (Plate II). Some explanation of this divergence in growth was sought and found partially in the behavioral history of the animals. Individual No. 650495 showed aggressive behavior from the date it hatched. It is the only one of the three pythons that has attempted to bite. All three animals initially had to have food placed in their mouths to induce them to eat, but python No. 650495 was the first one to start feeding by itself. Number 650503, which showed signs of aggressiveness only when forcedly excited, was the second individual to start feeding by itself. Python No. 650496 could not be induced to bite and never took food voluntarily.
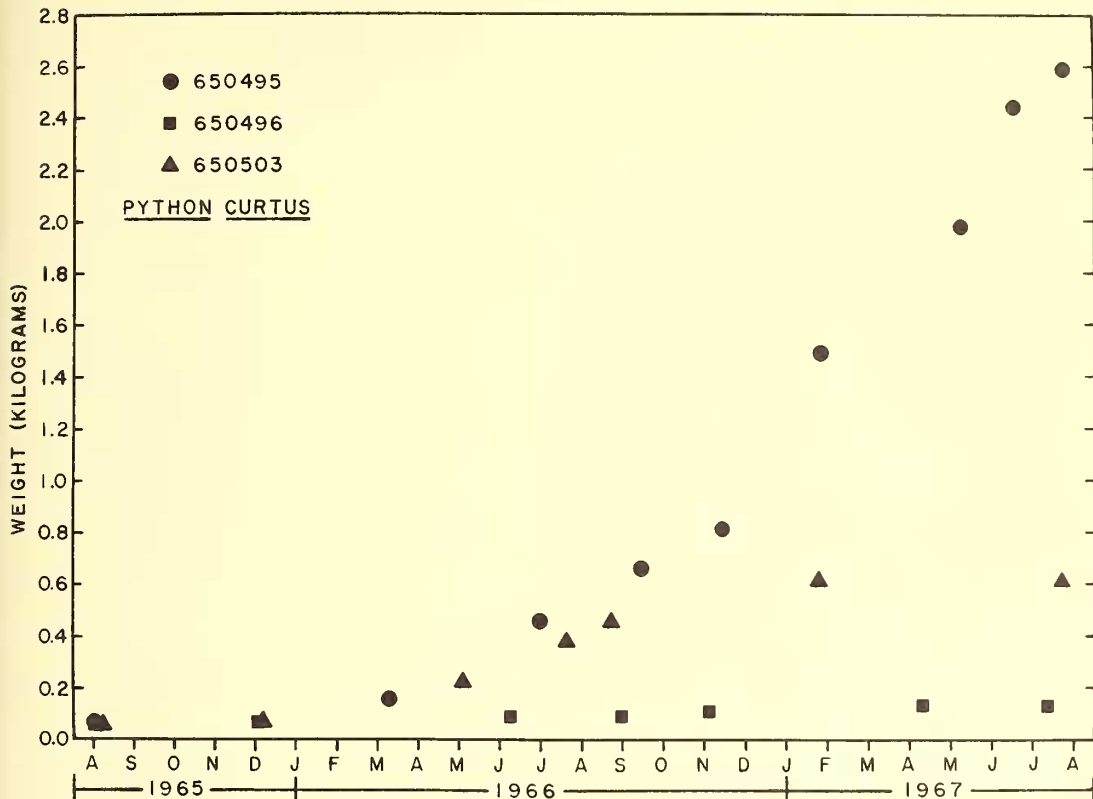
TEXT-FIG. 20. Growth of three hatchling *Python curtus* over a two-year period.

Table 3 summarizes the feeding and growth data of the three pythons for their first two years of life. The data for No. 650496 show the very slow rate of growth for each weight period. A slight loss of weight occurred for two periods, indicating that the food consumed since the previous weighing was enough to sustain life but not enough for additional growth. Individual No. 650495 shows a much higher growth rate; the maximum for one period was 9.18 grams gained per day for a 74-day period compared with a maximum of 0.27 grams gained per day for a 65-day period for No. 650496. The rates of growth for No. 650503 are intermediate between the other two animals. Another factor contributing to the difference of size attained by these animals is shown in Table 3. Data are shown which express the amount of food consumed which goes into producing new python protoplasm. These data are expressed as weight gain divided by food consumed times 100. The values based on total weight gain and total food consumed are for No. 650495, 52 percent; No. 650503, 45 percent; No. 650496, 29 percent. Not only was No. 650496 not consuming as much food as its siblings, but the low value of

29 percent indicates it was not using food as efficiently as the others.

Caloric values of the intestinal and renal wastes of the pythons are summarized in Table 4. Laboratory mice under 10 grams (wet) had a caloric content of 5204.39 ± 92.25 calories per gram (dry), while those over 10 grams (wet) had a caloric content of 5460.15 ± 48.34 calories per gram (dry). The specimen of *Python sebae* weighing 173.69 grams (wet) had a content of 4136.22 ± 67.51 calories per gram (dry). The ratio of dry weight to wet weight for the mice was 0.27, for the python, 0.21. Oxygen consumption of *Python curtus* is summarized in text-fig. 2. The caloric values, oxygen consumption data, and growth figures can be used to calculate an energy budget for the pythons over any growth interval for which there is complete data. Table 5 shows such an energy budget for each of the three pythons.

Discussion of Reptile Energetics

Pope (1965) gave an account of an Indian python, *Python molurus,* eating 123 laboratory rats (61 pounds) during its second year and most of its third year. The snake increased its

TABLE 3.

FOOD CONSUMPTION AND GROWTH OF THREE YOUNG *Python curtus* HATCHED FROM SAME CLUTCH OF EGGS.

Date	Days Since Last Weight	Weight g	Gain/ Day g	Weight Gain g	Gain X 100/ Food	Food Consumed (wet) g	Food Size g	Food Accumul.	Number of Food Animals
						Animal No. 650495			
1 VIII 65		69.7							
9 III 66	220	159.75	0.41	90.05	52	171.89	12.28(2.01-33.81)	171.89	14 mice
30 VI 66	113	455.00	2.61	295.25	60	494.81	30.93(23.06-35.32)	666.70	16 "
14 IX 66	76	656.09	2.65	201.09	52	388.28	29.87(22.70-36.72)	1054.98	13 "
14 XI 66	61	810.56	2.53	154.47	41	381.06	127.02(81.68-184.60)	1436.04	3 rats
27 I 67	74	1490.00	9.18	679.44	51	1319.63	164.95(98.50-244.72)	2755.67	8 "
8 V 67	101	1980.00	4.85	490.00	45	1084.51	216.90(184.33-240.50)	3840.18	5 "
18 VI 67	41	2440.00	11.22	460.00	64	722.92	180.73(101.90-260.02)	4563.10	4 "
25 VII 67	37	2590.00	4.05	150.00	26	570.57	285.29(257.05-313.52)	5133.67	2 "
						Animal No. 650496			
1 VIII 65		56.50							
2 XII 65	123	69.81	0.11	13.31	64	20.81	3.47(1.80-5.00)	20.81	6 mice
9 VI 66	189	92.75	0.12	22.94	33	68.65	3.43(2.00-9.17)	89.46	20 "
31 VIII 66	83	92.30	-0.0054	-0.45		27.36	3.04(2.16-4.58)	116.82	9 "
4 XI 66	65	109.86	0.27	17.56	40	44.34	2.61(1.24-4.95)	161.16	17 "
10 IV 67	157	130.23	0.13	20.37	22	92.50	2.50(1.32-4.07)	253.66	37 "
12 VII 67	93	129.76	-0.0051	-0.47		39.43	3.94(1.61-11.50)	293.09	10 "
						Animal No. 650503			
7 VIII 65		58.30							
6 XII 65	121	73.36	0.12	15.06	70	21.59	3.08(2.18-4.32)	21.59	7 mice
3 V 66	148	232.40	1.07	159.04	53	299.19	21.37(9.30-29.58)	320.78	14 "
20 VII 66	78	383.53	1.94	151.13	55	273.75	27.38(17.67-31.94)	594.53	10 "
23 VIII 66	34	460.09	2.25	76.56	50	151.90	30.38(29.13-32.62)	746.43	5 "
25 I 67	155	614.78	1.00	154.69	50	309.83	30.98(22.58-34.78)	1056.26	10 "
23 VII 67	179	608.99	-0.0323	-5.79		175.29	29.22(16.78-43.60)	1231.55	6 "

TABLE 4.

WEIGHT AND CALORIC VALUES OF WASTE PRODUCTS FROM
THREE SIBLING *Python Curtus* OVER A TWO-YEAR PERIOD.

Date	Sample	Dry Weight g	% Ash	Ash-free Dry Wt. g	Calories/ g	Calories/ (Ash-free) g	Total Calories in Sample
Animal No. 650495						
15 XII 65	Defec.	0.46	10.95	0.41	5094.06	5720.76	2343.27
9 III 66	Defec.	4.64	31.12	3.20	3483.59	5056.61	16163.86
26 VI 66	Defec.	15.11	29.32	10.68	3653.99	5170.92	55211.79
14 IX 66	Defec.	12.71	29.53	8.96	3517.79	4991.12	44711.11
14 IX 66	Uric A	11.03	5.62	10.41	2645.04	2802.41	29174.79
14 XI 66	Defec.	14.60	35.30	9.45	3084.18	4765.49	45029.03
14 XI 66	Uric A	16.02	2.57	15.61	2734.80	2807.03	43811.50
27 I 67	Defec.	49.12	36.59	31.15	3057.01	4820.63	150162.62
27 I 67	Uric A	54.35	4.85	51.71	2664.96	2800.73	144840.58
23 IV 67	Defec.	42.14	35.07	27.36	3134.35	4828.73	132081.51
23 IV 67	Uric A	43.58	5.54	41.17	2631.54	2785.85	114682.51
18 VI 67	Defec.	19.95					
18 VI 67	Uric A	23.55					
13 VII 67	Uric A	2.16					
25 VII 67	Defec.	34.09					
25 VII 67	Uric A	27.30					
Animal No. 650496						
2 XII 65	Defec.	0.29	10.08	0.26	5324.24	5920.97	1544.03
21 III 66	Defec.	0.76	27.92	0.55	4183.93	5804.62	3179.79
8 VI 66	Defec.	0.67	23.03	0.52	4201.13	5457.92	2814.76
19 VIII 66	Defec.	0.75	30.03	0.52	3660.76	5232.05	2745.57
4 XI 66	Defec.	0.63	25.89	0.47	4020.47	5424.84	2532.90
21 III 67	Uric A	1.37	2.55	1.34	2694.78	2765.23	3691.85
10 IV 67	Defec.	1.85	31.43	1.27	3643.02	5312.53	6739.59
10 IV 67	Uric A	0.41	5.19	0.39	2453.23	2587.39	1005.82
5 VI 67	Uric A	1.55	2.08	1.52	2699.87	2757.19	4184.80
28 VI 67	Uric A	0.70					
12 VII 67	Defec.	1.76					
12 VII 67	Uric A	0.42					
Animal No. 650503						
6 XII 65	Defec.	0.41	12.28	0.36	5028.39	5732.27	2061.64
3 V 66	Defec.	8.40	35.34	5.43	3403.81	5264.04	28592.00
3 V 66	Uric A	7.73	3.04	7.50	2709.68	2794.76	20945.83
20 VII 66	Defec.	9.27	28.17	6.66	3724.23	5184.51	34523.61
20 VII 66	Uric A	8.65	4.77	8.24	2668.64	2802.23	23083.74
23 VIII 66	Defec.	6.13	32.88	4.11	3259.58	4855.59	19981.23
23 VIII 66	Uric A	4.35	6.88	4.05	2549.74	2738.03	11091.37
25 I 67	Defec.	10.96	31.57	7.50	3417.19	4993.99	37452.40
25 I 67	Uric A	13.32	2.97	12.92	2735.01	2818.77	36430.33
23 VII 67	Defec.	5.79					
23 VII 67	Uric A	8.94					

weight by 34.5 pounds which is a gain of one pound for every 1.77 pounds of food or an efficiency of 56 percent. Barton and Allen (1961) gave data for an anaconda, *Eunectes murinus,* which when received was 16 feet 4 inches and 108 pounds. Over the next 81 months the snake ate 539 pounds of ducks and gained 92 pounds (one pound gain per 5.86 pounds food). This represents an efficiency of 17 percent. An African python, *P. sebae,* received at slightly over two feet consumed 148 pounds of food during its seventh, eighth, and ninth years of captivity (37 months) and gained 19 pounds, or 7.8 pounds of food for each pound of body weight gain for an efficiency of 13 percent. Brown (1958) found food efficiencies of 28 percent after one year, 34 percent after two years, and 20 percent after five and six years for *Natrix sipedon sipedon.* Food efficiencies for *Spalerosophis clifford:* were given by Dmi'el (1967). Data are broken down by age groups and sex. Animals under one year had efficiencies

TABLE 5.
ENERGY BUDGET FOR THREE SIBLING *Python curtus* OVER A TWO-YEAR PERIOD

Animal No.	650495	650496	650503	650503	650503	650503
Dates	30 June 66	4 Nov. 66	6 Dec. 65	3 May 66	20 July 66	23 Aug. 66
	14 Sept. 66	10 Apr. 67	3 May 66	20 July 66	23 Aug. 66	25 Jan. 67
Days	76	157	148	78	34	155
Budget (in % of total energy available)						
Growth	27.9	6.1	24.7	28.3	28.6	13.7
Maintenance and Movement	60.3	91.2	66.4	59.2	58.1	78.8
Intestinal Waste	7.1	2.3	5.1	7.4	8.6	3.8
Renal Waste	4.7	0.3	3.7	5.0	4.8	3.7
Total Energy	100.0	99.9	99.9	99.9	100.1	100.0

for males and females of 21 percent and 22 percent; one- to three-year animals, 26 percent and 33 percent; four- to eight-year animals, 11 percent and 23 percent; nine- to 13-year animals, 7 percent and 12 percent. The above data show that, after animals reach a certain age (size?), less energy is expended in growth and more in maintenance.

Pope (1962), in discussing the natural superiority of efficiency in pigs, mentioned that "the domesticated pig attains its size more rapidly than does any other barnyard animal, and on less food, too." Vanschoubroek et al. (1967) summarized the literature containing data for fully-fed pigs. The values are given as kilogram feed per kilogram gain and range from 3.17 to 4.09. These represent efficiencies of 31.5 percent to 24.4 percent, but the food provided was of optimal quality to promote growth with little non-digestable material. Data cited by Broady (1945) for cattle and sheep when calculated as efficiencies give a value of 9.6 percent. The pig with its high food conversion efficiency still is not as efficient as the pythons. There are two probable reasons for the high efficiency of pythons. First, being ectotherms they do not have to expend as much energy in maintaining high metabolic levels (brooding excepted). Second, because they are rather sluggish except when looking for food they expend less energy in activity. A python in the wild would probably expend more energy in activity since food is not as readily available as under captive conditions.

Various aspects of lizard energetics have been considered by some authors. The effects of prolactin on growth of adult male *Anolis carolinensis* were studied by Licht and Jones (1967). The energetics of food intake and growth were evaluated. Caloric contents of food items were calculated and corrected for fecal losses. These figures were used to calculate average calories assimilated per animal per day. The data re-

calculated for control animals show that those weighing about 5.2 grams at 32°C on a 14-hour photoperiod in the spring assimilated 54 to 63 calories per gram-day; 5.7-gram animals at 32°C on a six-hour photoperiod in the winter assimilated 26 to 42 calories per gram-day; and 5.4 gram animals at 32°C on a 14-hour photoperiod in the winter assimilated 12 calories to 17 calories per gram-day. Animals in the spring, having normal appetites, show caloric intakes which agree well with the results of Johnson (1966) and McNab (1963).

Johnson (1966) dealt with one aspect of the energetics of three species of lizards *(Sceloporus undulatus, S. magister,* and *Cnemidophorus tigris),* namely, assimilation. His data are based on analyses of stomach contents. The weight of food eaten is estimated from these analyses. The caloric value of grasshoppers (5363 calories per gram) as determined by Golley (1961) is taken as representative of all food items. The energy assimilated by a 15-gram *S. undulatus,* a 22-gram *C. tigris,* and a 30-gram *S. magister* is estimated at 0.83 kilocalories, 1.57 kilocalories, and 2.17 kilocalories per day (55 calories, 71 calories, and 72 calories per gram-day), respectively.

McNab (1963) estimated an energy budget for a 19-gram *Sceloporus undulatus* and made some comparisons with a *Peromyscus maniculatus* of the same weight. The estimate involves these assumptions: the body temperature drops at night; the body temperature is regulated at a mean of 35°C by behavioral means during the day; the lizard is active about one-fifth of the daylight hours; and its active metabolism is about 2.5 times its resting metabolism. Recalculated data of Bartholomew and Dawson (1956) show that a 19-gram lizard uses about 1.12 kilocalories per day, of which 23 percent (0.26 kilocalories per day) is used in activity. The estimate of active metabolism being 2.5 times

standard metabolism may be low (Dawson and Bartholomew, 1958). McNab pointed out that a 19-gram *S. occidentalis* uses about 0.26 kilocalories per day for activity compared with a 19-gram *Peromyscus maniculatus* which uses about 1.70 kilocalories per day; the mouse thus uses 6.5 times more energy. In spite of the greater energy collected by the mouse, it is unlikely that 6.5 times more energy is needed for food gathering.

Surface Area-Weight Relationships

Benedict (1932) attempted to relate surface area to weight for a series of snakes. His determinations of surface area were obtained by measuring distances from the nose and corresponding girths and then taking mean values of these measurements to calculate area. Then, assuming that surface area $= K$ weight$^{0.67}$, Benedict proceeded to determine K for each snake. The mean value of K for a series of eight snakes of several species weighing 3.49 kilograms to 13.21 kilograms was 12.5 and ranged from 12.0 to 13.2. Values of 14.3 and 14.4 obtained for a 31.80-kilogram python on two separate occasions were discarded by Benedict because they were "probably a little too large." A value of 17 was obtained for the 5.58-kilogram 1931 python which was the only surface area determined directly from the skin. Benedict compared his K values with those of Inaba (1911) which were obtained from five snakes ranging in weight from 48 grams to 109 grams. The values were 19.1, 17.0, 17.5, 18.7, and 19.9, with a mean of 18.6. Benedict attributed the difference between his values and those of Inaba to the fact that Inaba skinned his animals, thereby stretching the skin. However, values of K from the present study range from 23.1 and 24.7 for animals weighing 132.6 grams and 166.1 grams to 10.8 for a 99-kilogram animal. From these data it would seem that K varies inversely with weight and is a constant only within limited ranges of weight. These observations are consistent with those of Meeh (1879). He stated that K is a constant only for a group of similarly shaped animals.

Benedict (1932) and Inaba (1911) assumed that area is proportional to weight to the 0.67 power. However, the actual relationship for a series of seven pythons was determined by calculating a regression of surface area on weight (text-fig. 21). This resulted in the equation $A = 43.16\ W^{0.549}$, where 0.549 is significantly different from 0.67 at the 95 percent level. Thus, the actual proportionality between surface area and weight must be determined by calculation rather than by assuming that the coefficient of weight is 0.67.

Surface Area-Length and Weight-Length Relationships

For a given length, *Python molurus* is a thicker snake than *P. reticulatus*. Plots of surface area against length (text-fig. 22) and weight against length (text-fig. 23) show this relationship. Data for *P. sebae* are included in the latter figure which show that its shape is closer to *P. molurus* than to *P. reticulatus*.

Physiological and Ecological Implications of the Geographic Distribution of *Python molurus* and *Python reticulatus*

Licht and Moberly (1965) found that a temperature near 30°C is required for development of the eggs of the green iguana, *Iguana iguana*. Temperatures a few degrees above and below 30°C resulted in death of the embryos. Their concluding statement that ". . . these results illustrate the need for careful attention to the thermal requirements of the eggs in consideration of the ecology and distribution of lizards," can apply equally to snakes. It becomes of particular significance when applied to the distribution of pythons. For the Indian python, *Python molurus,* to have a well developed system of physiological thermoregulation while brooding its eggs suggests that the additional heat supplied to the eggs may be needed to prevent them from reach a critically low temperature.

The mainland distribution of *Python molurus molurus* includes peninsular India from Sind, West Pakistan, and Punjab in the northwest to Bengal in the northeast. *Python m. bivittatus* is found over the whole Indo-Chinese subregion. It is recorded as far south as Zinba Chanun, Tavoy district, Burma. It has been collected to the north in the region of Yenping, Fukien, China, in the east and in Yuankiang, Yunnan, China, and Myitkyina, Burma, in the west. *Python reticulatus* is found on the mainland in southern Burma and Thailand as far north as latitude 18°; to the east as far north as Yen-Bai, North Viet Nam; to the south, throughout Malaysia (Pope, 1935; Smith, 1943). These distributions are shown in text-fig. 24 with some of the specific localities mentioned above plotted on the map. The distribution of these pythons conforms closely with the zoogeographical areas set up by Smith (1931). The area of sympatry corresponds to Smith's Annam area in the east and Indo-Chinese Great Plain area in the west. North of the area of sympatry is Smith's Trans-Himalayan Mountainous area.

The factor limiting the northern distribution of *P. reticulatus* may be the critical minimum temperature for the development of its eggs. Unfortunately, data on minimum temperature

S.A. = 43.16 W$^{0.55}$
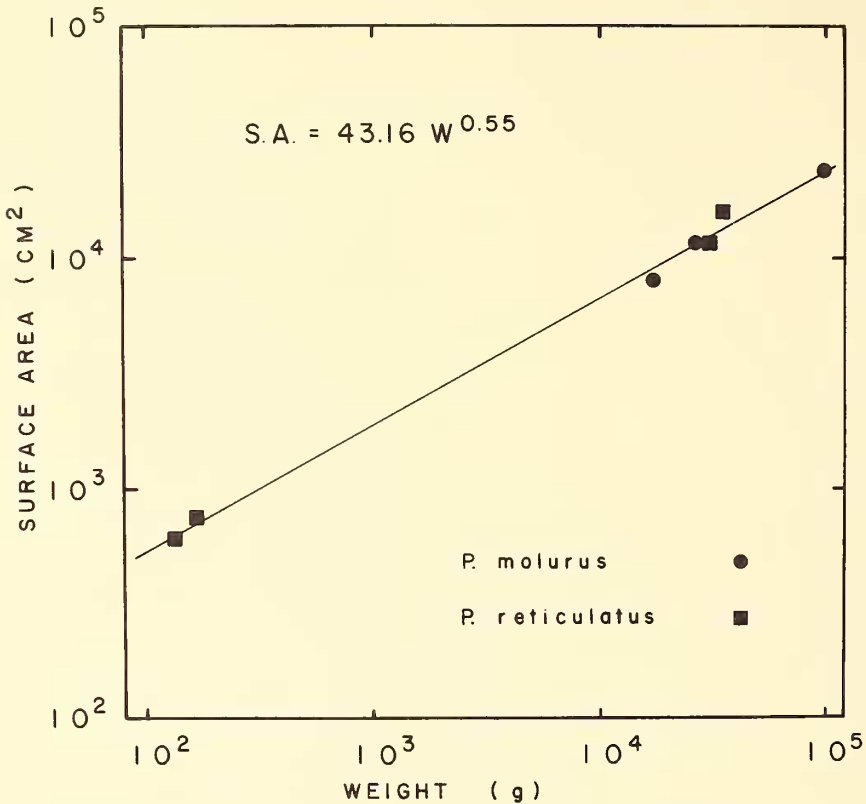
TEXT-FIG. 21. Correlation of surface area with weight of two species of pythons *(Python molurus* and *P. reticulatus)*. Line and regression equation calculated by method of least squares.

requirements of python egg development are scarce. Some indication of the requirements for the hatching of *Python sebae* eggs was given by Joshi (1967). He separated a clutch of 28 eggs into four batches. Five of seven of the eggs kept at 72°F to 84°F (22.2°C to 28.9°C) and 65 percent to 80 percent relative humidity hatched in 52 days. Four eggs kept at 86°F to 90°F (30.0°C to 32.2°C) and 80 percent to 90 percent relative humidity hatched in 49 days. Eggs kept at 70°F to 90°F (21.1°C to 32.2°C) and less than 40 percent relative humidity did not hatch. The last batch kept surrounded by moist soil in a dry sunny place did not hatch, but no temperature or humidity data were given. Although the times that the eggs were at the lower temperatures are not provided, it appears that temperatures as low as 72°F (22.2°C) are not deleterious to the eggs as long as the humidity is fairly high.

In addition to better information on temperature requirements of egg development, information is also needed on climate for the regions where these snakes are found. The distributions of *P. molurus* and *P. reticulatus* correspond roughly with the surface temperature regions of Parkins (Espenshade, 1964). *Python reticulatus* ranges through the area of hot summers and winters, while *P. molurus* is found also in the regions of hot summer and mild or cool winters (hot = above 20°C; mild = 10° to 20°C; cool = 0°C to 10°C).

These data support the hypothesis that distribution of these two pythons is limited by egg development temperature. However, additional data are needed to substantiate this hypothesis.

GENERAL DISCUSSION

Colbert, Cowles, and Bogert (1946) determined heating rates of alligators by tethering them in the sun and recording their cloacal temperatures. They demonstrated a 1°C/1.5 minute (6.6 x 10^{-1} °/minute) increase in temperature for a 50-gram alligator and a 1°C/7.5 minute (1.3 x 10^{-1} °/minute) increase for a 13,000-gram alligator with 260 times the body mass. They interpolated to find a 1°C/86 hour (1.9 x 10^{-4} °/minute) temperature rise for a nine-million-gram dinosaur, having 700 times the body mass of the large alligator. In a later paper (Colbert, Cowles, and Bogert, 1947) they de-

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fended objections made to their interpolation. The objectors had pointed out that surface area, mass, and heat capacity must be taken into consideration. The recalculated times for a 1°C rise were 67 minutes (1.5 x 10⁻² °/minute) from one person and 66 minutes to 81.5 minutes (1.5-1.2 x 10⁻² °/minute) from the other. The authors admitted their original figure was derived incorrectly but insisted that the time would still be as long as several hours rather than the low figures submitted. They claimed that the alligator cannot be treated as a cylindrical, inanimate mass but that various physiological processes must be considered. Bartholomew and Tucker (1963) gave an example of what effect physiological processes have on heating and cooling in the agamid lizard, *Amphibolurus barbatus.* They compared the heating and cooling rates of live and dead lizards. The live lizards heated more rapidly than they cooled, thus showing some physiological control. However, the cooling rate of the live lizards was still more rapid than the heating and cooling rates of the dead lizard. This would tend to support the objections raised against the conclusions of Colbert, Cowles, and Bogert. A live animal with physiological control of its heating and cooling rates heats up more rapidly than a dead animal. Therefore, a live animal should also heat up more rapidly than an inanimate model having the same thermal conductivity.

The demonstration of physiological thermoregulation in some lizards (Bartholomew and Tucker, 1963, 1964; Bartholomew, Tucker, and Lee, 1965) and of physiological thermoregulation and thermogenesis in pythons (Hutchison, Dowling, and Vinegar, 1966) suggests that mechanisms of physiological thermoregulation occurred in some of the large primitive reptiles and did not originate *de novo* in mammals and birds.

Rodbard (1949) discussed the possibility that the large membranous sail-like structures of the Permian reptiles *Dimetrodon* and *Edaphosaurus* were used as absorbers of solar radiant energy. An argument for dinosaurs having had some sort of physiological thermoregulation was presented by Russell (1965). He first established that the dinosaurs were intermediate between birds and crocodilians and in many ways closer to birds in their skeletal anatomy. Then assuming that the similarities are carried through to their soft anatomy, he suggested that dinosaurs had separate arterial and venous circulations and therefore, some degree of homoiothermy.

Cys (1967) refuted Russell's hypothesis of endothermy in the dinosaurs, stating that its presence is not necessary to explain dinosaur extinction. Instead, Cys maintained that the large size of dinosaurs prevented them from finding hibernation sites. Russell (in a comment at the end of Cys, 1967, p. 267) pointed out that several dinosaurs were certainly small enough to find hibernation sites. He summarized his comments by stating that there appears to be some "flaw" in dinosaur make-up, relating to their extinction, that is independent of size, shape, feeding habits, or systematic position. Proving that the "flaw" is homoiothermy may not be possible, but the hypothesis fits much of the available evidence.

The ability of large ectotherms to maintain body temperatures above ambient is not confined to reptiles. Carey and Teal (1966) demonstrated that tuna (big eye, *Thunnus obesus,* and yellowfin, *T. albacares*) can maintain elevated body temperatures with a countercurrent heat exchange system located in the vascular system of the red muscle masses. The heat exchanger provides a thermal barrier which prevents heat from being carried off by the blood and lost through the gills. Maximum temperatures found were 32°C in a 70 kilogram *T. obesus* from 20°C water and 26°C in a 12 kilogram *T. albacares* from 19°C water. The objection that the high internal temperature results from the fish struggling on deck was disproved by experiments with curarized fish and measurements of free-swimming fish.
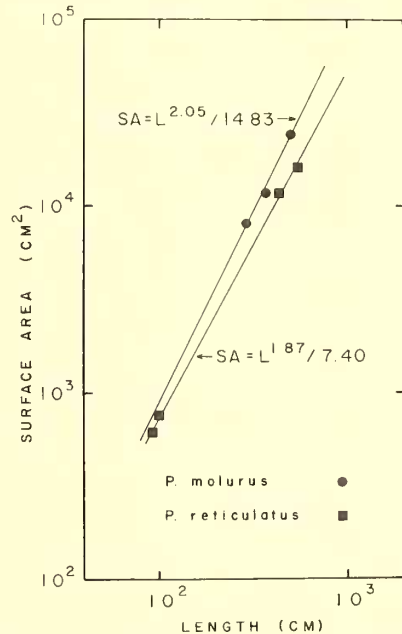
TEXT-FIG. 22. Correlation of surface area with length of two species of pythons *(Python molurus* and *P. reticulatus).* Lines and regression equations calculated by method of least squares.
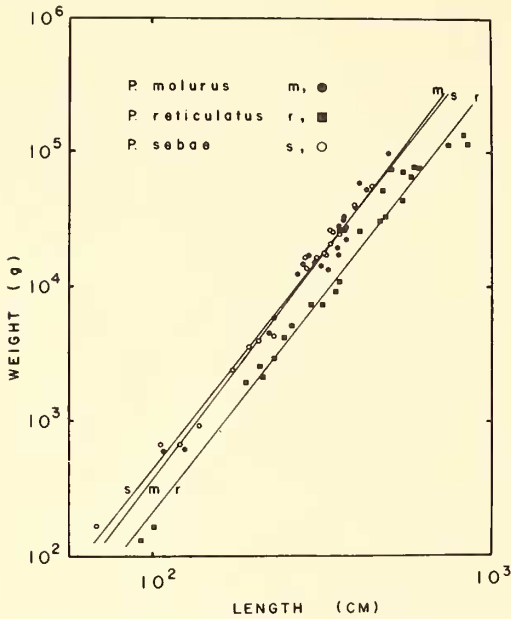
TEXT-FIG. 23. Correlation of weight with length of three species of pythons *(Python molurus, P. reticulatus* and *P. sebae)*. Lines determined by method of least squares.

$$P.\ molurus - W = (L^{3.358})/14180$$
$$P.\ sebae - W = (L^{3.217})/6155$$
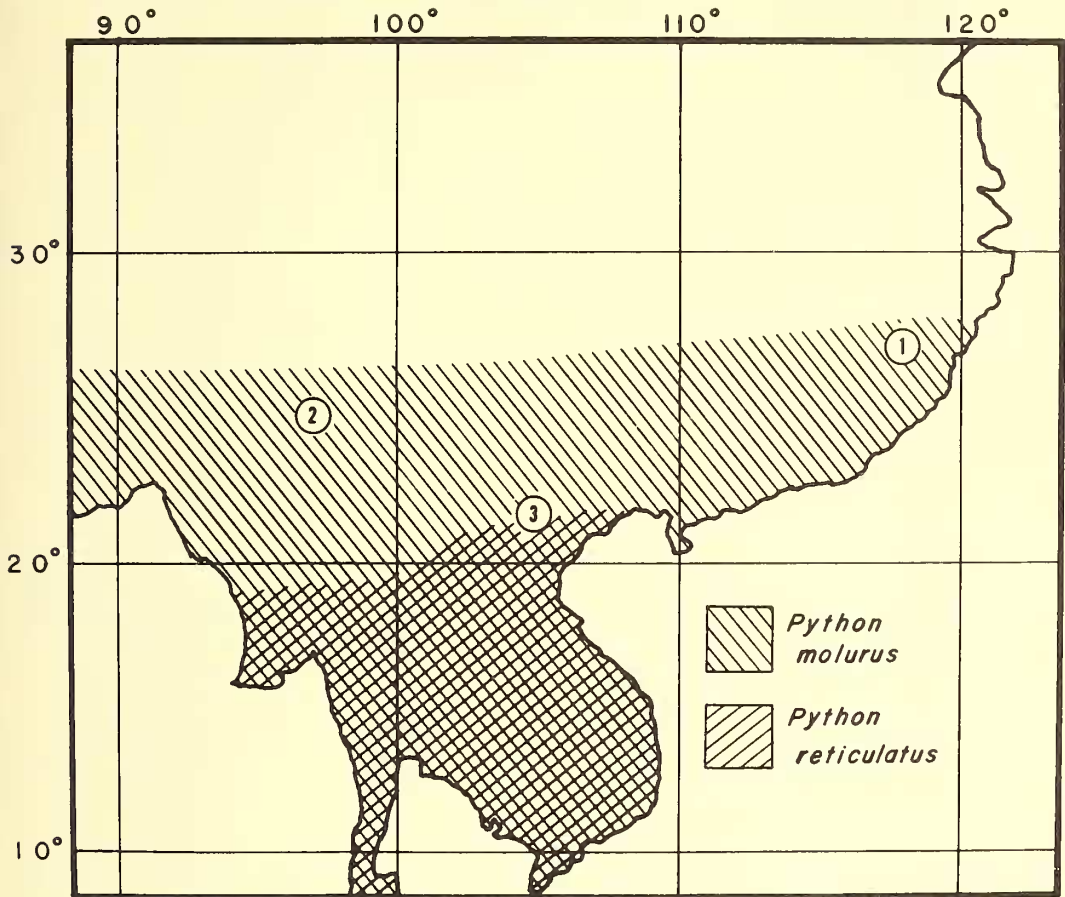$$P.\ reticulatus - W = (L^{3.231})/13750$$

Tied in with the ability to regulate body temperature is the ability to sense the temperature of the environment. A temperature sensitive center, with maximum sensitivity at the level of the third ventricle of the brain, was demonstrated in *Pseudemys elegans* by Rodbard, Samson, and Ferguson (1950). Warming of the area resulted in a rise in blood pressure and cooling resulted in a fall in pressure. Evidence for a temperature control center located in the head was given by Heath (1964); he demonstrated head-body temperature differences in *Phrynosoma coronatum* with the head 3°C to 5°C higher in partially buried animals and 2°C to 4°C higher in active animals. Emergence of these lizards possibly is dependent on head temperature and independent of body temperature. Hammel, Caldwell, and Abrams (1967) demonstrated that the behavioral regulation of body temperature in the blue-tongued skink, *Tiliqua scincoides,* is dependent on a combination of hypothalamic and other body temperatures. This demonstration was made by implanting thermodes across the preoptic region of the brainstem and heating and cooling this area while the lizard was at environmental temperatures of 15°C or 45°C. Further experiments on *Tiliqua scincoides* (Cabanac, Hammel, and Hardy, 1967) demonstrated five "warm neurons" which increase their activity with rising brain temperature and three "cold neurons" which increase activity with falling brain temperature. These neurons are located in the preoptic region of the brain.

The similarities in temperature sensitivity between the brains of mammals and reptiles point to the possibility of reptilian brains having contained the progenitor of the more finely developed hypothalamic thermostat of mammals. Rodbard (1948) discussed some of the evolutionary implications of blood pressure changes in response to body temperature changes. These responses were noted in chickens, rabbits, turtles, and frogs. Rodbard suggested that the first amphibians coming onto land encountered greater diurnal changes in temperature than did the ancestral fish. Thus, the function of hypothalamic sensitivity was to adjust metabolic activity to body temperature changes. This hypothesis is supported by the work of Cabanac et al. (1967), Hammel et al. (1967), and Heath (1964). The function of the hypothalamus for the fine control of body temperature probably came with the development of homeothermy in mammals and birds. The thermoregulation of brooding pythons may represent an intermediate step in the development of the latter function for the hypothalamus. Bligh (1966) speculated on the significance of the earlier function of the hypothalamus as a "broad-band" control in modern mammals. He suggests that the remnant of the "broad-band" control, dependent only on thermal sensitivity of the hypothalamus, may act in the case of emergencies as during fever, heat and cold stress, and intense activity. The 24-hour shift in deep body temperature demonstrated in water-deprived camels (Schmidt-Nielsen et al., 1957) may be an example of "broad-band" dominance. Similarly, the diurnal or seasonal heterothermy of various mammals may be derived from the early "broad-band" control (Twente and Twente, 1964).

ACKNOWLEDGMENTS

TEXT-FIG. 24. Distribution of *Python molurus* and *P. reticulatus*. Western part of range of *P. molurus* and island distribution of both species not indicated. 1 — Yenping, China; 2 — Myitkyina, Burma; 3 — Yen-Bai, North Viet-Nam.

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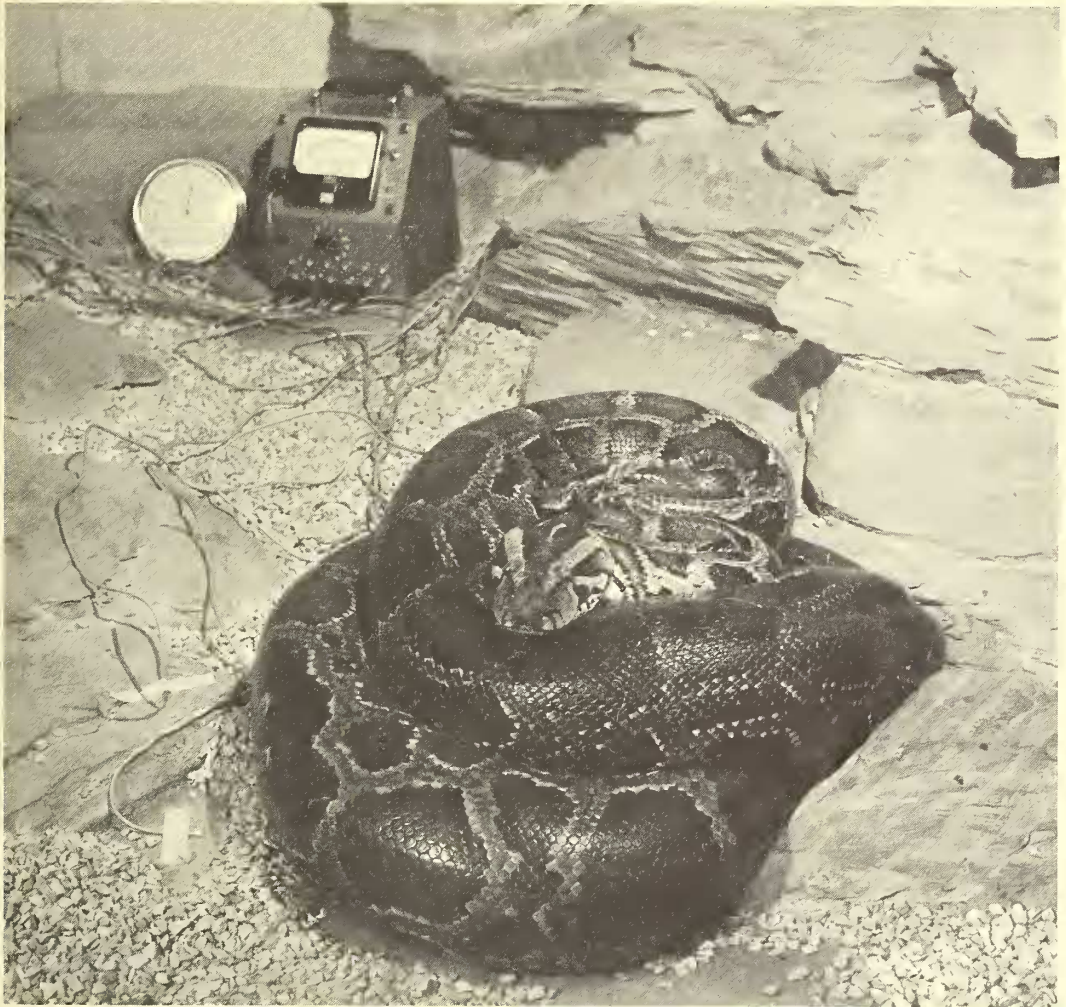
EXPLANATION OF THE PLATES

PLATE I

Brooding *Python molurus bivittatus* (NYZS Photo). (Vinegar, Hutchison, Dowling).

PLATE II

Three members of a single brood of *Python curtus* (William Meng Photo). (Vinegar, Hutchison, Dowling).

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